# THE FREE-LIVING UNARMORED DINOFLAGELLATA

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BY

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## PREFACE

The collections upon which this study has been based were made off the coast of southern California, in large part from June to August, 1906, and from June to September, 1917. Preliminary observations on a number of the more common and hardier species found in the inshore plankton have been carried on, mainly during the summer months, over a series of years by the senior author; in 1901–1903 at the summer Marine Laboratory of the University of California at San Pedro and at Coronado Beach; in 1904–1907 at the Marine Laboratory of the San Diego Marine Biological Association and in 1907–1917 at its successor, the Scripps Institution for Biological Research at La Jolla, and at the Naples Biological Station in January-May, 1908, while occupying the table of the Smithsonian Institution.

Additional opportunities have been afforded to the senior author in the Agassiz Expedition to the Eastern Tropical Pacific in 1904–1905, and in the plankton traverse of the Northern and Western Pacific and Indian oceans during a trip from San Francisco to Colombo, Ceylon and return in 1916, to widen his knowledge of the dinoflagellates generally. The immediate results of these observations are not, however, included in this paper.

The junior author, who has been associated with the enterprise since July, 1915, spent the summer of the two subsequent years at La Jolla, in work upon these and other dinoflagellates. In June to September, 1917, the most intensive work was done upon the naked dinoflagellates. The junior author spent three months at La Jolla, with Miss Anna L. Hamilton as colorist, and was joined by the senior author during the six weeks while the material was most abundant.

Much assistance was rendered in the earlier years by Mrs. Effie J. Rigden Michener, and in the summer of 1914 by Miss Inez Smith, who made a careful investigation of the dinoflagellate fauna of the beach sands. In the summer of 1917 Miss Rofena Lewis, Miss Pirie Davidson, Miss R. E. Merrill and Miss E. H. Logan gave material assistance in seeking for the elusive organisms and in preliminary analyis.

The authors are especially indebted to Miss Anna L. Hamilton, to whose artistic skill in the use of water colors and faithfulness in interpreting our analytical sketches, our plates owe whatever technical merit they possess. We are also indebted to Miss Rofena Lewis for much valuable assistance in the preparation of the bibliography and much of the clerical work connected with the preparation of the material.

Most of all, our work owes its origin and continuance to Professor William E. Ritter, Director of the Scripps Institution, for it was he who encouraged the beginning of this work many years ago, and has generously fostered its continuance and completion with the facilities and resources of that institution, made possible by the generosity and continued interest of its donors, Miss Ellen S. Scripps and Mr. E. W. Scripps.

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# INTRODUCTION

The dinoflagellates form an exceedingly important part of the ocean meadows, the source of the primitive food supply of the sea, both in the number of individuals and in the total mass of living substances produced. They abound both in neritic waters and in the high seas and range from the tropics to the polar oceans. As synthetic producers of carbohydrates, proteins, and fats they hold high rank among the protists of the sea and of fresh water. In abundance they are second only to the diatoms in the marine plankton, while locally and in midsummer they may far outnumber even these abundant organisms. At their periodic maxima they may surpass the diatoms in the total mass of substance produced and in the rapidity of their development. These local massive developments are the primary and all but universal cause of the discolored seas, and of the phenomenon of the "Mare Sporco," or luminescent waters, which are wont to occur in midsummer in neritic regions and on the high seas, especially in the tropics and along the western shores of the American continents. Similar extensive growths of fresh-water dinoflagellates, especially of *Ceratium*, cause reddish discolorations in reservoirs and lakes in midsummer.

The phenomenon of the phosphorescence of the sea has been known since Pliny (see Bostock and Riley, 1885) noted the fact that "there are sudden fires in waters." But the organisms which are responsible for the most of the light in the ship's wake and in the breakers along shore have been studied but little, and the light they shed is often erroneously attributed to the Copepoda or exclusively to *Noctiluca,* while in reality it may often be due to other dinoflagellates.

No monograph on the Dinoflagellata is included in the reports of the Challenger Expedition, and *Pyrocystis*, the most brilliant dinoflagellate of the high seas, was described by Sir John Murray as a diatom. Even our most widely known *Textbook of Zoology* (Parker and Haswell) erroneously ascribes to the neritic genus *Noctiluca* the phosphorescence of the high seas.

The purpose of this monograph is to set forth a summary of our present knowledge of the most elusive and least known representatives of the dinoflagellates, namely, the naked or unarmored forms. Many of these are most brilliantly colored, vying with the orchids and butterflies in variety of color and delicacy of shading, although microscopic in size. They also include some of the most highly organized and uniquely specialized of the greatly diversified group of Protozoa, presenting species possessing, among other organs, a structurally complicated eye with lens, pigment mass, and sensory core, also a mobile tentacle-like structure, and nematocysts not less specialized than those of the coelenterates. These highly specialized species exist moreover within a group of protists in which holozoic and holophytic nutrition occur in different species within the same genus. The great fundamental function of nutrition has not

in the dinoflagellates reached that definite degree of differentiation which delimits the animal and vegetable kingdoms. On this basis botanists and zoologists alike will continue to regard the dinoflagellates as within the legitimate scope of their several fields. The present paper increases the evidence for a much greater representation of holozoic forms among the dinoflagellates than has been hitherto known. Much confusion has accordingly arisen in the study of Dinoflagellata due to the fact that the group contains both holozoic and holophytic organisms, with the result that the literature dealing with them has been divided between the botanical and zoological fields, with a consequent lack of correlation.

Furthermore, the organisms themselves, as shown above, are usually exceedingly sensitive to adverse conditions on removal from their normal habitat, do not long survive microscopical examination, and are subject to progressive changes as dissolution approaches. As a result these pathological conditions have sometimes appeared in the figures and descriptions as normal phases of form and function. This is especially true of the delicate, pelagic representatives of this group. It is hoped that the present paper will be of use in clearing up some of the obscurities which still remain regarding a number of species of the group.

This monograph also sets forth the authors' conceptions of the relationships of the genera within the group, which differ materially in a number of particulars from those of previous investigators in this field. One feature of some significance is the re-alignments necessitated by the discovery that *Pyrocystis*, at least as originally described by Murray (1876), is only a phase in the life history of other Dinoflagellata, e.g., *Gonyaulax*. A second feature is the separation of *Noctiluca* from the Cystoflagellata Haeckel (1873) and its inclusion in the Noctiluciidae, merely a family of the order Diniferidea. The gap which has long separated these from the Dinoflagellata has been so completely bridged by discoveries, some of them long overlooked, such, for example, as the significance of Hertwig's (1876) *Erythropsis*, that the isolation of *Noctiluca* and related forms in a separate order, or even suborder (Jollos, 1910), is no longer defensible.

The reasons for the slow development of our knowledge of this remarkable group of organisms are their eupelagic habitat and the correlated fact that they are but poorly represented in the neritic plankton. Few marine biological stations are so located that they have quick and ready access to the pelagic life of the open sea, and the fresh-water species of the Gymnodinioidae are relatively few and show little differentiation. An additional reason lies in the fact that their period of maximum occurrence is in midsummer and that the area of greatest abundance is in the warm temperate and, presumably, the tropical seas. The main reason, however, is to be found in the exceedingly delicate and sensitive nature of the organisms themselves. The turmoil of the filtering water in the plankton net, the crowded state of the plankton collection, and even the conditions of aëration on the microscopic slide are all hazardous in the extreme to the soft and flexible bodies of these dinoflagellates. Mutilated

individuals of such delicate species as *Gymnodinium rubrum* were almost as abundant in our plankton collections as were normal ones.

These species are also noticeably sensitive to illumination and under conditions of microscopical examination undergo cytolysis rather quickly. Some of the more delicate ones succumb in a few moments after exposure to the intense illumination of the high-power microscope. Others survive for a longer time, though rarely for as much as an hour, while in every case the organisms begin to round up, lose very quickly their characteristic contour, distinctness of sulcus and girdle, and normal color and distribution of pigment or other colored substances, in the confinement of the microscope slide. The result is that as soon as the organisms quiet down sufficiently to permit observation and analysis of structure they begin to give more or less distorted pictures of their real organization. The rounding up and increasing vacuolation which attend the initial phases of cytolysis are evident in many published figures of species in the group, including some in this paper.

Other reasons for the lack of observations on the Gymnodinioidae are the rapidity of locomotion and incessant movements of many of the species, especially of the smaller forms. The larger ones, such as *Noctiluca*, readily permit observation since flagellar activity is slight with reference to the total mass of the organism, and both rotation and locomotion are relatively feeble in this and other large forms. On the other hand, there are a host of minute forms which have thus far eluded pursuit, or, if pursued by the aid of the mechanical stage, they never stay quiet long enough at a time to permit observation, much less an accurate drawing. We have not found it possible to make use of any anaesthetic or fixing agent to bring these active forms under observation. The few more resistant species, such as *Polykrikos schwartzi* and *Gymnodinium lira*, which survive the diffusion currents resulting from the admixtures of sea water and the chemicals used in fixation, are more or less contracted and distorted, while the majority of species are wholly disrupted or mutilated and contracted beyond recognition by attempts at fixation for cytological study. The cytoplasm of these organisms is so nearly labile that the use of any of the known cytological and protozoological methods has thus far failed to preserve their structure satisfactorily for subsequent staining, mounting, and permanent preservation of specimens. There are therefore few if any type specimens in existence of species in this group.

The investigator of the group is thus limited to the primitive and simple method of observation of the living organism in action. This has its advantages, for while we may not determine the finer cytological detail as preserved more or less imperfectly in the coagulated and sectioned substance of the organism, we do have, under such conditions of examination of these active and mobile dinoflagellates, a near approach to the normal form, and in most cases an exceptional transparency of the living substance, which makes possible an analysis, in the natural state, of internal structure, to a degree of completeness which is rarely equaled in the investigation of the Protozoa.

The discovery of the unusual amount of material of this group which has been made by us in the waters off southern California is in part due to the oceanographic conditions prevailing in our field of operations. These are seen in the eupelagic area, that is, typical ocean water of the high seas, little modified by tributary streams and free from dominating coastal influences such as are created by a much indented coast line or an extensive archipelago.

The temperatures during the months of July and August at the surface of the sea off La Jolla range from nineteen to twenty-one degrees Centigrade (McEwen, 1916). These are characteristic of warm temperate seas. The salinities are free from disturbances by discharge from rivers or by local rains during this season. The upwelling of waters from below against the coast, and apparently also against the steep slopes of the outer limits of the continental shelf, enriches the surface levels off the California coast with nitrogenous compounds brought up from the depths of the sea. Evidences of this enrichment are to be seen in the wealth of the pelagic fisheries, in the submarine forests of giant kelps, and in the recurrent outbreaks of red water due to the rapid development and consequent enormous numbers of dinoflagellates, usually of *Gonyaulax polyhedra*, which recur yearly off the shores of southern California, especially from July to September.

An additional oceanographic factor favoring the occurrence of the warm water fauna off southern California during the summer months is the influence of the inshore, north-bound, return current which moves northward along Lower California in an increasing volume and to a higher latitude as the season advances to the culmination of its northward flow in December or thereabouts. This tends to bring more tropical contributions to the offshore plankton, as well as to bring about a rise in temperature.

This combination of stable, favorable oceanographic features constitutes an ideal environment for these delicate organisms, attuned as they are to environmental changes of small amplitude. Owing to the rapid increase in depth offshore and to the slight modifications of the shore line, the conditions of the littoral zone adverse to pelagic life are confined to a relatively narrow belt off the California coast, so that the pure water of the high seas with its fairly stable conditions of temperature and salinity, and freedom from detritus and continental wastes, is to be found within a few miles of the laboratory of the Scripps Institution for Biological Research at La Jolla. Few institutions and few localities in the world are so favorably located for the study of this group as is the laboratory at La Jolla.

## Material and Collections

The material upon which these studies are based was obtained for the most part in the summer of 1917, from June 1 to August 25. The organisms were obtained in the first place in towings made with a plankton net of No. 12 silk towed at the surface along the new pier at the Biological Station, about one

thousand feet offshore. Collections were taken at intervals of four hours throughout the day and night. In addition to these collections another series was made intermittently during the summer of 1917 at distances of two to five miles offshore over depths of one hundred to six hundred fathoms.

The success we have attained in securing the striking representation of the group here revealed has been due to the opportunity to get living material promptly into the laboratory from oceanic conditions some distance offshore. This was accomplished in the summer of 1917 by certain modifications of the earlier methods, which had involved the use of short tow nets of No. 20 silk bolting cloth with an opening of fourteen inches in diameter and a length of about forty inches. The amount of plankton taken in these was large, and presumably only the hardier species survived the crowded conditions and the delay attendant upon bringing in the collection by the slow motor boats then in use. In 1917 a smaller net, five inches in diameter and fifty inches in length, of No. 25 silk bolting cloth (the equivalent of No. 20 of earlier years in having approximately 40,000 meshes per square inch) was adopted. This was lowered to a depth of eighty meters, three to six miles offshore, towed at that level slowly for twenty minutes and then brought to the surface by hand. The bottom of the net terminated in a four-ounce, wide-mouthed bottle, which was tied in the end by a lashing and served as a detachable plankton bucket. The catch was transferred at once to a quart jar of fresh sea water and hurried to the laboratory by speedy motor boat for examination, with the result that these delicate animals were found in unprecedented frequency and exceptionally fine condition.

The amount of plankton during the summer months of 1917 was at no time large, and often the catch in the bottle was so small as to be scarcely visible to the naked eye. For this cause, as well as by reason of the small orifice of the net, the catch was small, and owing to the relatively large filtration surface, computed to be four times the area of the orifice, the rate of movement of the water through the minute orifices of the silk was not rapid enough to destroy the delicate Gymnodinioidae of the plankton. Furthermore, owing to the absence of crowded conditions in our small catches and to the fact that the "Ellen Browning," the fast boat of the Biological Station, has a speed of thirty miles an hour, it was possible to convey the catch to the laboratory in a quite normal condition.

A list of the earlier collections, most of which have been examined in fresh and preserved condition, will be found in Ritter *et al.* (1915, p. 156) in the list of *Preliminary plankton collections*. Preserved collections of plankton are of no value in the study of this group except for records of the occurrence of a few of the more highly resistant and specialized forms, such as *Polykrikos* and *Gymnodinium lira*, and even these are rarely found in such collections. Most species do not survive the ordinary application of reagents used in preservation, such as formalin.

## Methods

The necessity of working to a very large extent with living material, and the very limited numbers of individuals to be found of any one species of the group, except *Polykrikos schwartzi* and *Noctiluca miliaris*, have determined the methods employed, and have excluded cytological investigations and any consideration of life histories.

Promptly upon arrival in the laboratory the plankton was examined in Syracuse dishes under the low power, and when some representative of the group was detected it was isolated with a fine pipette, placed on a slide under a cover glass and located with the aid of a mechanical stage. When its activities were slowed down it was usually possible to determine its dimensions by the aid of the camera lucida, or even to get an outline of its more evident structures. Interpretative sketches, color notes, and other details were generally obtained before the rounding up, cytolysis, and death of the organism occurred. It was not always possible to get all the details from one animal, or in some cases to determine all the desirable points in the brief time of observation. This fact explains some of the deficiencies in our accounts of these interesting animals.

Colors are recorded in the system of nomenclature of colors proposed by Ridgway (1912). Certain very puzzling difficulties arise in any attempt to use these plates of Ridgway's with organisms illuminated by transmitted light under the microscope. Changes in the diaphragm, in the focus of the condenser, in the objective used, or even in the source of light, all affect the color values of the object. The same object may have very different color tones under these changing conditions of illumination. Furthermore, it is impossible to find in the Ridgway color samples the exact equivalents of all the colors of the dinoflagellates when thus viewed. The brilliance and delicacy of the coloring of these transparent objects is not reproduced in the opaque tones of the color samples.

The varying refractive indices of the contained fat bodies and other refractive substances, and the color modifications induced by the rapid accumulation of a pinkish fluid in a peripheral zone of vacuoles as cytolysis impends, all combine to increase the difficulty of giving a correct interpretation of the color values of these particolored organisms. In view of the reduction in color values due to the amount of light necessary for observation with the higher powers of the microscope and to the color changes due to approaching death, it is probable that the colors as portrayed in our plates are not exaggerated, and are, in some cases at least, much less brilliant than they are in nature.

Much aid in the trying process of pursuing these incessantly moving organisms has been secured by the use of the high-power, binocular microscopes of Leitz and of Bausch and Lomb. These have also proved invaluable in the analysis of the complicated furrows and girdles of this group and in revealing the true contour of the surfaces.

## CHAPTER I

# GENERAL MORPHOLOGY: SIZE AND FORM, MOTOR ORGANELLES, FURROWS AND TORSION OF THE BODY

The Gymnodinioidae are among the least known of all the dinoflagellates for several reasons. They are in the main found in oceanic waters or at least where neritic influences are not potent. This pelagic habitat affords the second reason for the obscurity surrounding the group, to wit, the very great delicacy of the organisms and their extreme sensitiveness to adverse conditions. At the best it is highly improbable that all the forms belonging to the group survive the turmoil of the plankton net, the changes in salinity, temperature, pressure, illumination, ionization and proportions of dissolved gases incident upon the transfer from the open sea to the film of water beneath the cover glass, and to the concentrated light of the high-power microscope. For many of them dissolution ensues within a few moments after they are placed under the microscope for observation, with explosive abruptness and utter disruption of all structural features, while even hardier forms contract more or less, undergo profound color changes and lose their characteristic features very soon after exposure to the axial rays of the microscope.

One of the results of the great susceptibility of these organisms to slight environmental changes has been the frequent appearance in the literature dealing with these forms of figures of abnormal character, caused by changes incident to microscopical examination. Another point which must be considered not only in studying the organisms themselves, but in any review of the literature dealing with them, is the great transparency of their bodies and the trap which may thus be set for even experienced biologists. The importance of this fact lies in the liability of the operator to mistake the opposite side of the organism under the microscope for the side nearest him or uppermost, with the result that the orientation of the organism is completely reversed. There are many instances of such reversed orientation recorded in the literature (Kofoid and Swezy, 1917) even among veteran investigators, as that of *Nematodinium armatum* (= *Pouchetia armata*) by Dogiel (1906), where the girdle is drawn as though extending from the ventral face to the right of the body and over dorsally to the left, a complete reversal of its actual course.

These conditions call for caution in dealing with the group, even where an abundance of material and a variety of forms have been present, as in our own work on these organisms. Some of the pitfalls have been avoided, but others unwittingly may have been overlooked.

For the convenience of the reader the following brief outline of the Dinoflagellata is here given. The group contains two orders, the Adiniferidea without a girdle and the Diniferidea with a girdle. The former contains two tribes, the Athecatoidae, without cuirass, as *Haplodinium*, and the Thecatoidae, with enveloping cuirass, as *Prorocentrum*. The Diniferidea are likewise divided into two groups, the Gymnodinioidae or naked forms and the Peridinioidae or armored forms, such as *Peridinium*. Both of these groups contain a few species of doubtful relationships. The Gymnodinioidae contains seven families, to wit, Protodiniferidae, Gymnodiniidae, Polykrikidae, Noctilucidae, Pouchetiidae, Blastodiniidae, and Cystodiniidae.

In the following discussion of the tribe Gymnodinioidae the chief emphasis is laid upon those members of the group comprised in the families Protodiniferidae, Gymnodiniidae, Pouchetiidae and the genus *Pavillardia* in the Noctilucidae. Attention is not confined, however, to these forms alone, but illustrative material is drawn upon from the entire Dinoflagellata where pertinent to the subject in hand.

Size and Form.—As a group the Flagellata probably has a smaller average size for its members than most of the other large groups of Protozoa. The two subdivisions of this group which attain the maximum size found within it are the Trichonymphidae and the Dinoflagellata, and of these two the latter presents some of the greatest variations in size found within the group, having, at one end of the scale, the largest individuals and, at the other end, some of the smaller, though not the smallest ones, thus far described for the Flagellata.

Within the Gymnodinioidae (excepting *Noctiluca*) these variations in size extend from 11$\mu$ to 212$\mu$ for the motile flagellated individuals, but some of the parasitic forms attain a length of 700$\mu$. The maximum size within the group is, however, attained by *Noctiluca*, which may have a transdiameter of 1 to 1.5 mm. The average length for members of the Gymnodiniidae is about 100$\mu$. The greatest size in this family is found in the more specialized members of *Gymnodinium*, such as *G. pachydermatum* and *G. dogieli* (figs. AA, 5, 8), and in *Cochlodinium*, such as *C. strangulatum* (fig. GG, 8). Next to these in size comes the Pouchetiidae, whose largest members are somewhat smaller than the largest members of the other group, but whose smallest members do not reach the lower extreme in size (figs. KK–RR), all the species being nearer the average than are the species in the other genera, *Gymnodinium*, *Gyrodinium*, and *Cochlodinium*.

The variations in size within the species cannot be stated with any degree of certainty, owing to the lack of knowledge of the amount of growth that may take place within a single developmental cycle, and often also to the small number of individuals of a single species that can be found, even with prolonged searching. In forms which are obviously members of a single species, variations of a third, or slightly more, may sometimes be noted in the length.

Other factors which make a determination of the variation in size within the species very difficult are the extreme sensitiveness and ready response of

these delicate organisms to slight environmental changes. These responses are usually shown in the form and dimensions of the body. It is only in comparatively rare cases that an individual may be kept under observation under the microscope long enough for a complete camera drawing, without these changes in the body manifesting themselves. Often indeed they have begun when the drop of water containing them is first imprisoned by the cover slip (fig. A).

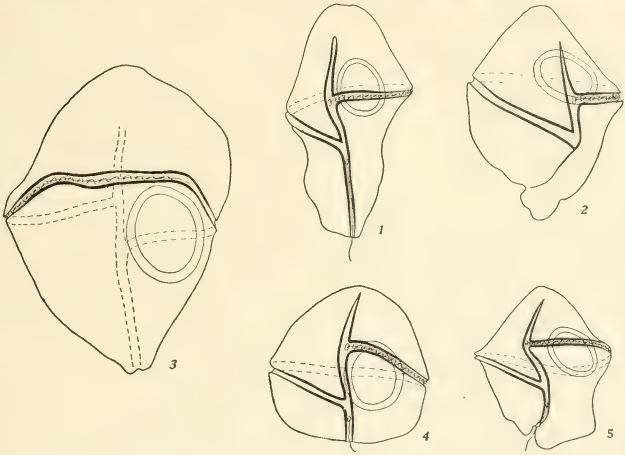


Fig. A. Variations in size and shape of *Gymnodinium rubrum* sp. nov. 1. Individual showing the normal appearance of the body. 2–5. Individuals all taken from the same haul and showing variations in size and shape. × 355.

These changes consist of a gradual but slight increase in diameter and a progressive rounding up of the body, with obliteration of the furrows, ending in complete disruption of the entire organism. The rounding up or thickening of the body, resulting in a diminished length and increased diameter, is a common condition in plankton hauls that have remained in the laboratory for half an hour or more, particularly if any great length of time has elapsed between the actual taking of the haul and its appearance in the laboratory. In hauls containing an abundance of material this degenerative process is much more rapid than where the change from the more highly oxygenated oceanic waters is not emphasized by overcrowding.

The same effect may sometimes be produced by the ingestion of large food bodies, that is, the body becomes shorter and broader to accommodate the food mass (pl. 5, fig. 56). After the process of digestion is completed the body gradually resumes its normal shape and size.

The shape of the body of the lower members of the dinoflagellates approaches that of the typical flagellate, that is, a slender pear-shape with the flagella attached at the anterior end. This is shown in *Haplodinium* (fig. R, 5). Starting out from this simple type the first changes are found in the gradual shifting of the location of the flagella, which may have their origin at any point between the anterior and posterior ends of the body (fig. R). With this backward shift of these organelles the form of the body responds to the change by assuming a spindle-shape, which is the predominant one among the dinoflagellates, though often secondarily modified, as in the dorsoventral compression of the body in many species of *Amphidinium*.

Further modifications of this primary shape are found in the extension of the labile posteroventral sulcal area of *Cochlodinium* and *Pouchetia*, culminating in the prod of *Erythropsis* (fig. T). This latter genus is further modified by the thickening of the body, giving it a squat appearance typical of all the members of the genus (pl. 12). A few species of *Gymnodinium* (figs. X, 7, 8, 26) seem to have acquired a permanently rounded form.

One of the most striking and characteristic features of the body is its bilateral asymmetry, following the rule obtaining throughout the Protozoa generally, where complete bilateral symmetry is the exception outside of some of the Radiolaria. This bilateral asymmetry is directly correlated with the spiral course in locomotion, and may be one of the factors in the maintenance of the organism near the surface of the sea. Kofoid's studies (1910*b*) on the thecate dinoflagellates point to the conclusion that optimum conditions of existence for the members of this group lie within the upper levels of more or less illuminated water, and that descent below this region is fatal for them. The apparent lack of special organs for flotation, other than vacuoles, is compensated for by the asymmetry of the body, and in the thecate forms, where a greater appreciable overweight of the body is present, by the formation of horns and fins. These combined with the rotation of the body caused by its asymmetry impede the descent of the organism into lower regions in response to gravity. Having a lighter specific gravity and greater powers of locomotion, the need for additional structures to meet this response is less insistent in the naked dinoflagellates than in the thecate forms.

An increasing torsion or twisting of the body, beginning with the genus *Gyrodinium* (figs. CC–EE), reaches its culmination in the genus *Cochlodinium* (figs. FF–HH), where the twisting of the body, as shown by the course of the girdle, may be as great as four complete turns, as in *C. augustum* (fig. HH, 15). This is correlated with the movements of the flagella, combined with the pressure exerted by the water on the more plastic species of the genus. In the thecate forms this backward reach of the distal end of the girdle has not developed beyond the *Gymnodinium* and *Gyrodinium* types, showing either a loss of plasticity in the body structures accompanying the relatively slight locomotor powers of the skeletal-bearing forms, or else indicating the origin of these forms from ancestors similar in lack of torsion to these two genera in the Gymnodiniidae.

MOTOR ORGANELLES.—The most important structures of the protozoan organism, from a systematic point of view, are its motor organelles. In the Flagellata these consist of flagella and vary in number and position in the different groups. The dinoflagellates are characterized by the presence of but two flagella of different types, transverse and longitudinal, each having its own definitely located position, and, in the case of the transverse flagellum, a structure peculiar to this group. The longitudinal flagellum is threadlike in form, trailing after the body, and held more or less rigidly in position, or waving in broad curves (fig. B, *long. fl.*) or with intense terminal activity. It arises from the posterior pore (fig. B, *post. p.*) in the sulcus, in case there are two pores, and its proximal part lies in the ventral sulcus (*sulc.*) near the major axis. The transverse flagellum (fig. B, *tr. fl.*), on the other hand, runs around the body in a nearly transverse plane, arising from the anterior pore near the proximal end of the girdle (fig. B, *ant. p.*) and is often, if not always, ribbon-like in form; it moves in a close-set spiral, or undulating wave of contraction, and is usually lodged in a deep, encircling groove, wound in a flat or more or less steep spiral from the left ventral face around dorsally to the right side in a more or less complete girdle of one or even several turns (fig. C). In the Adiniferidae and in a few other isolated cases both flagella arise from the same pore placed at or near the anterior extremity of the body (fig. R, 7). In the majority of forms the two flagella arise from two different pores on the ventral surface, and not infrequently at considerable distances from each other (fig. C, 10).

The transverse flagellum itself consists of a deeply staining thread or stout fibril, bordered on one side by a comparatively wide, finlike sheet of transparent protoplasm or membrane, somewhat greater in length than itself, and thrown into ripples or folds of wider amplitude than the fibril. This is in constant, wavelike motion progressing from the proximal end distally. Reversals in direction have occasionally been noted. The flagellum arises from a large deeply staining blepharoplast situated somewhat below the surface of the body. Accurate cytological investigation of its internal relationships has not thus far been made with any degree of success.

This fundamental organization of the motor organelles may be obscured in several ways. In the Adiniferidae the girdle and sulcus are not developed (figs. R, 5–7), although the nucleus is of the dinoflagellate type, as are also the two flagella the form and function of which are strikingly suggestive of those of the dinoflagellates included in the Diniferidae. They also possess a porulate theca in the tribe Thecatoidae. In *Protodinifer* (fig. R, 2) the very faintly developed girdle clearly forecasts the fundamental relationships of this organ found in the remainder of the dinoflagellates. It probably represents the beginnings of the development of these peculiar relations within the group.

In the Diniferidae this fundamental organization is sometimes obscured by the interposition of long encysted stages, with a consequent shortening of the dinoflagellate stage of the life cycle, by secondary loss of the flagella with the

addition of new organelles, and by parasitism, with its resulting profound modifications of the entire organism.

In those organisms included in the old group Pyrocystidae (or Pyrocystaceae), which probably represent typical encysted phases in the life cycle of certain genera of the dinoflagellates, the encysted stage or period has become prolonged, while the free, motile gymnodinium-like stage is reduced to a relatively short period (fig. I). It is in the free, motile stage, usually obscured in the huge, inflated sphere of the encysted organism, that its relationships to other dinoflagellates and the usual details of its specific organization must be looked for. The details of the loss of flagella and their subsequent outgrowth in these stages have not been followed. In the ordinary encysted stage of the Gymnodiniidae both flagella are apparently absorbed at the beginning of encystment, and towards the end of the period may be seen as very short outgrowths, indicating a new formation for both flagella. The possibility of their being cast off is not precluded. It is not uncommon to find encysted individuals with neither longitudinal nor transverse flagella present.

A still more profound modification has taken place in the little known group of parasitic dinoflagellates. The free, motile stage, which is brief, and alone shows the genetic relationships of the species, has the characteristic organization of *Gymnodinium*, with the typical motor organelles (fig. J, 5). With the beginning of a parasitic career these are lost and the organism becomes a huge non-motile, sacklike structure infesting the tissue of its host (fig. J, 1).

In *Protodinifer* (fig. R, 2), *Pavillardia* (fig. JJ), *Noctiluca*, and most strikingly in *Erythropsis* (pl. 12), the development of a tentacle or prod has resulted in the loss or almost complete disappearance of the longitudinal flagellum. An occasional individual, with both flagella in addition to the prod in *Erythropsis*, as in *E. minor* (pl. 12, fig. 131), confirms the suspicion that this condition is only a secondary modification. In *Noctiluca* the transverse flagellum also has been reduced in size and lies in a short groove which soon fades out and is probably the remnant of a girdle (fig. KK), though the inflation of the body makes its exact status difficult to determine.

The normal function of the prod of *Erythropsis* in the usual habitat of the animal is not made evident by the activities observed. *Erythropsis* is a eupelagic organism. It is a member of a group of dinoflagellates, none of which, excluding *Amphidinium*, so far as evidence at hand goes, ever has normally any relation whatever to the substrate. Moreover, as far as our limited observations go, it could not compare with the usual flagellar equipment of the Gymnodinioidae as an organ of propulsion in free-swimming movements. It might give a spasmodic thrust to the body, but its presence, in *E. extrudens* (pl. 12, fig. 130) especially, constitutes a serious impediment to locomotion, at least in the extended state, since it considerably increases the resistance of the body to the water, and, unless thrown back into a trailing position, its asymmetry, with respect to the main axis of rotation and progression, is formidable.

Two other functional possibilities of this prod remain. The prod may be either a feeding or a defensive structure. The energetic retractions combined with the capitate end of the tentacle would tend to press any object against the ventral furrow if caught between it and the body on its anterior face. *Erythropsis extrudens* has no chromatophores. No food bodies were noted in the individuals observed. Many if not all *Pouchetia, Cochlodinium,* and *Gyrodinium* are holozoic. Holozoic nutrition is indicated for this species also and the tentacle might be effective as an organ of ingestion.

Observational evidence is likewise lacking for the second function suggested above, namely, that of an organ of defense. In fact in all our observations on living holozoic Gymnodinioidae no instance of active capture and ingestion of food has been seen. It is obvious, however, from the size and activities of this tentacle that a marauding holozoic dinoflagellate, such as a *Pouchetia, Cochlodinium,* or the larger *Polykrikos,* or even *Noctiluca,* would find it rather difficult to capture, hold, and engulf a vigorously kicking *Erythropsis.* The function of the tentacle as an organ of defense is not incompatible with that of the capture of food, although the operation in either fashion involves contradictory internal states on the part of the organism, conditioned by hunger and satiety or by the nature of its contact with other organisms.

Another type of structure, the value of which as a motor organelle in these forms is problematical, is the peculiar form of pseudopod formation which has been described by Zacharias (1899) for a chromatophore-bearing *Gymnodinium, G. zachariasi* (fig. BB, 3). This has been cited by West (1916) as indicative of holozoic nutrition, but Zacharias offers no evidence that these structures are used in the capture of food or as motor organelles. They are outgrowths of the extremely plastic sulcal area, modifications of which are found in *Cochlodinium,* and *Pouchetia,* culminating in the prod of *Erythropsis* (fig. SS). The loss of the longitudinal flagellum in those forms in which the prod or tentacle is well developed might indicate that its function is, to some extent at least, subserved by the new organelles thus introduced. Evidence on this point, however, is lacking. Such retractile processes are not unlike those recorded by Rhodes (1920) for the holozoic polymastigote flagellate, *Collodictyon.* Similar pseudopodia-like processes are functional in this genus in capturing organisms for food.

Furrows and Torsion of the Body.—Closely connected with the motor organelles, both morphologically and in their evolutionary development, and equally important from a systematic point of view, are the furrows of the body of the dinoflagellate. They constitute its most striking structural features. All stages of development and elaboration of these peculiar and characteristic structures are found within existing species of the group, from the fine, faint traces in the lower forms to the spiral of three or four turns in the more specialized *Cochlodinium,* and to the elaborate furrows outlined by lists or fins of great beauty and delicacy of design in the thecate forms of *Gonyaulax, Peridinium,*

and *Ornithocercus.* It is in the non-thecate forms that the development and fundamental relations of the furrows may be most clearly seen.

These furrows are two distinct structures, the more conspicuous of which is the furrow or girdle passing around the body in a transverse direction (fig. B, *gir.*). Its course is that of a descending left-wound spiral, with the ends usually more or less widely displaced. The second furrow is a longitudinal one, the sulcus, connecting the ends of the girdle, sometimes continuing on to the apices (fig. B, *sulc.*). Its course is morphologically longitudinal and in most of the genera its increasing length keeps pace with the increasing torsion of the body. This gives it a spiral path around the body in the more highly specialized members of the group, as in *Cochlodinium* (figs. GG, HH).

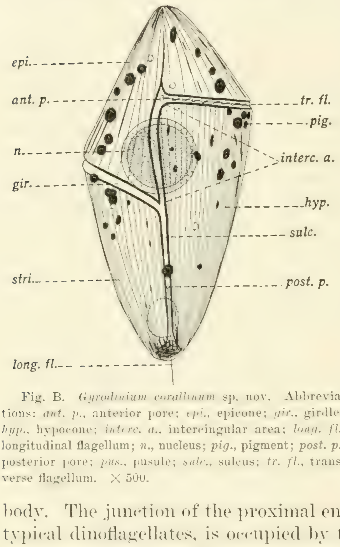


Fig. B. *Gyrodinium corallinum* sp. nov. Abbreviations: *ant. p.*, anterior pore; *epi.*, epicone; *gir.*, girdle; *hyp.*, hypocone; *interc. a.*, intercingular area; *long. fl.*, longitudinal flagellum; *n.*, nucleus; *pig.*, pigment; *post. p.*, posterior pore; *pus.*, pusule; *sulc.*, sulcus; *tr. fl.*, transverse flagellum. × 500.

These two structures, the girdle and sulcus, are usually present at some period of the life cycle of nearly every member of the Dinoflagellata outside of the Adiniferidea. In the latter the furrows are entirely lacking. In the genus *Protodinifer,* the most primitive of the Diniferidea (fig. R, 2), the girdle is merely incipient, short and poorly developed, its length being less than 0.3 transdiameter of the body. The sulcus connected with it is also short and feebly developed, and is occupied posteriorly by a stout, rodlike tentacle, which projects a short distance beyond the body. The junction of the proximal end of the girdle and sulcus here, as in the typical dinoflagellates, is occupied by the anterior pore from which issues the transverse flagellum. The transverse flagellum in *Protodinifer* occupies the girdle and continues its course around the body beyond the incipient girdle, its length frequently being greater than one complete turn. In the members of the Adiniferidea, such as *Prorocentrum* and *Haplodinium*, the anterior extremity of the body is marked by a shallow notch from which arise the two flagella (figs. R, 5, 7), without any indication of a girdle.

In the Diniferidea the girdle and sulcus are thus the outstanding features. In *Oxyrrhis*, a second primitive genus, the girdle is posteriorly located, its proximal border well developed, but not its distal one, resulting in a wide depression of the posterior portion of the body (fig. R, 3). The typical form of the girdle is first attained in the Gymnodiniidae, where it is usually complete

and well defined, with clearly marked, equal borders. Its length varies from 0.5 of a turn around the body in *Hemidinium* (fig. C, 1) to four complete turns in the more highly specialized species of *Cochlodinium* (fig. C, 10). It may form a complete circle about the body, as in a few of the simpler *Gymnodinium* (figs. X, 1, 2, 8), or its ends may become displaced, so that the distal end comes to lie nearer the posterior region of the body than to the proximal end, as in *Gyrodinium* (fig. CC). Its course thus becomes a more or less steep, spiral path around the body.

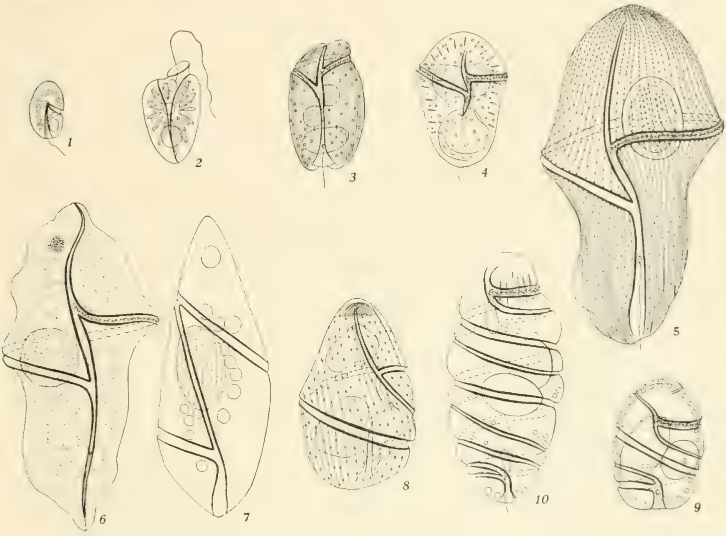


Fig. C. Types of girdle arrangement. 1. *Hemidinium nasutum* Stein. After Stein (1883, pl. 2, fig. 24). 2. *Amphidinium steini* (Stein). After Stein (1883, pl. 17, fig. 9), slightly modified. 3. *Amphidinium scissum* sp. nov. 4. *Gymnodinium doma* sp. nov. 5. *Gymnodinium rubrum* sp. nov. 6. *Gyrodinium spumantia* sp. nov. 7. *Gyrodinium contortum* (Schütt). After Schütt (1895, pl. 21, fig. 65). 8. *Cochlodinium pirum* (Schütt). After Schütt (1895, pl. 23, fig. 76). 9. *Cochlodinium clarissimum* sp. nov. 10. *Cochlodinium augustum* sp. nov. × 500.

With this posterior displacement of the distal end of the girdle an increase in length takes place which, in some of the species in *Gyrodinium,* becomes greater than one turn of the body (figs. CC, 22; DD, 17). This produces a torsion of the body which continues with the increasing length of the girdle until it may make two (fig. C, 9), three (fig. HH, 16), or even four complete turns of the body, which is the maximum length reached in *Cochlodinium* (fig. C, 10). Closely correlated with the length of the girdle and the resulting

torsion of the body is the torsion of the sulcus which of necessity is carried around the body in a spiral course, usually one turn less in length than that of the girdle (figs. GG, HH).

The increased length of girdle and sulcus, with the consequent torsion of the body, results in a profound modification of its dorsoventral plane. In *Gymnodinium*, which lacks appreciable torsion, the plane passing through the two flagellar pores marks the dorsoventral plane of the body and is longitudinal. These two pores are usually located at the junctions of the girdle and sulcus, the anterior pore at the anterior junction, the posterior pore at the posterior junction. The latter pore may frequently open into the sulcus posterior to the junction, but only rarely anterior to it.

In the simpler Gymnodinioidae these two pores are placed near together, as in *Oxyrrhis* (fig. R, 3), *Hemidinium* (fig. R, 4), many *Amphidinium* (figs. U, 2, 3, 10, 25), and *Gymnodinium* (figs. X, 2, 14). They still lie, however, in a longitudinal plane passing through both apices. In some species of the last two genera the pores have become widely separated (figs. U, 1, 4; X, 5; AA, 6), a condition which is common for the more specialized genera, as *Gyrodinium* (figs. CC) and *Cochlodinium* (fig. GG), as well as in the *Pouchetiidae*, where the ends of the girdle are more or less widely displaced. In these species, where appreciable torsion of the body is found, the morphologically dorsoventral plane, passing through the two pores, becomes correspondingly twisted, and ceases to lie in the geometrical longitudinal plane passing through both apices.

With the gradual increase in the length of the girdle in *Gyrodinium* and *Cochlodinium* the posterior end of the girdle is pushed farther around the body, carrying with it the posterior pore and sulcus, as well as the morphological ventral surface lying between the two pores. With the continued increase of the girdle up to two complete turns of the body, the morphological dorsoventral plane undergoes a corresponding torsion with these structures, although the general biconical or fusiform shape of the body as a whole differs little if at all from that of the non-twisted forms. As a result of the torsion, the ventral surface established by the presence of the sulcus follows the torsion of this structure in its one to four turns (as in *Cochlodinium augustum*) around the longitudinal axis of the body. Thus the position of the anterior pore alone does not determine the ventral face of the organism.

The sulcus represents the most mobile, plastic portion of the organism. It is the region for the ingestion of food and hence is capable of great distension, judging by the size of the organisms sometimes ingested. In *Cochlodinium roseaceum* (pl. 8, fig. 85) the ingested *Pouchetia* has a length of 0.48 of the length and a breadth of 0.33 of the transdiameter of the *Cochlodinium* which has mastered it. In *C. vinctum* (pl. 2, fig. 15) the food mass contained within its body has a length of 0.7 and a width of 0.41 of its own dimensions respectively. A still more striking instance is found in *Pouchetia voracis* (fig. PP, 2), where a thecate *Peridinium* has been successfully captured. The cytoplasm

had evidently been digested before it came under our observation, the remaining theca presenting the appearance of being crushed together and of massing near the posterior end of the body, preparatory to being ejected on the release of the organism from its cyst. *Peridinium* of this type are large organisms and the half shell still intact has a length equal to about 0.5 of the total length of the body of the *Pouchetia*, showing that the ingested organism was about equal in size to the marauder which had captured it. The length of the intercingular area in this species is about 0.5 of the total length of the body, hence its distension must have been enormous to enable it to grapple successfully with a food mass of this size.

In its simplest condition the sulcus is a shallow furrow joining the ends of the girdle, but this stage is relatively rare, as it usually presents various modifications. The anterior and intercingular portions of the sulcus usually present few variations of structural details beyond the apical loop. Its posterior extension may sink into the body, forming a deep excavation at the antapex, or it may even bifurcate the entire posterior half of the body, as in *Gymnodinium bifurcatum* (fig. AA, 3). In *Amphidinium* the sides are often drawn out into flaps which are thrown across the furrow and cover the opposite border (fig. 21, 5). It may also function in the production of pseudopodia (Zacharias, 1899), as in *Gymnodinium zachariasi* (fig. BB, 3), in the tentacle of *Protodinifer* (pl. 7, fig. 74), in the ventroposterior process of *Proterythropsis* (pl. 11, fig. 123), and in the prod of *Erythropsis* (pl. 12).

Its extreme mobility is undoubtedly correlated with its function as the mouth of the organism. The process of food-taking in the dinoflagellates is still a mystery. Many of the forms observed in the cytoplasm are those of active organisms and the means by which they are caught and held until the engulfing protoplasm receives them are puzzling in the extreme. The great mobility of the lips of the sulcus probably offers a solution to the puzzle. Saville-Kent (1880–82) observed *Gymnodinium marinum* actively devouring smaller monads in the culture with it, engulfing them at this region without the formation of pseudopodia. Critical evidence as to the exact nature of this activity in other members of the group is almost entirely lacking.

## CHAPTER II

# GENERAL MORPHOLOGY: NUCLEI, PUSULES, OCELLI, NEMATOCYSTS

Nuclei.—The Dinoflagellata are definitely marked off from the remainder of the Flagellata by certain features which are distinct and peculiar to the group. Two of these features, the furrows and the two types of flagella, have already been discussed. Another organelle no less peculiar is the nucleus with its moniliform chromatin threads, one of the most characteristic structures found within the group, and, in some respects, the most constant feature of its organization. It retains its typical appearance during encysted stages when the flagella are lost and the furrows have become obliterated (fig. P) and forms the only distinguishing mark of the organism.

Its appearance in the living organism is usually remarkably clear and distinct. Schütt, in his monograph on the dinoflagellates (1895), clearly illustrates its structure in very many members of the group. It is usually relatively large, varying from spheroidal to ellipsoidal in shape, sometimes greatly elongate as in *Torodinium* (fig. II), and slightly curved to conform with the contour of the body (pl. 10, fig. 115). The latter type is more frequently found in the thecate forms, but in both cases is probably only a predivision stage. The relative size may vary considerably in individuals of the same species.

The nucleus is surrounded by a distinct membrane which is often double-contoured. In a few species it is surrounded by a wide zone of clear, homogenous appearance (pl. 6, fig. 63), which in others, as in *Gyrodinium corallinum* (pl. 10, fig. 117), may be filled with large, fairly regular alveoli. In the living organism its chromatic contents present an organization of moniliform threads, the constituent granules of which are rather coarse and closely pressed together in linear rows (fig. X). The chromatin threads may be variously arranged, coiled, or in parallel rows, and fill the entire nucleus. The threads vary in length with the size of the nucleus and usually follow its longer axis in more or less of a spiral with the ends of the threads sometimes apparent at the poles of the nucleus. Nucleoli may be present, lying imbedded in the mass of chromatin threads (fig. U, 10).

The structure of the nucleus varies but little in the different groups. In *Erythropsis* the chromatin network is rarely visible in the living form, the nucleus presenting that glaucous appearance noticeable in the entire organism (pl. 12).

The position of the nucleus is generally near the center of the body, though this may vary greatly throughout the different groups. Its position may also be changed by the presence of ingested food bodies within the cytoplasm.

Nuclear division in the dinoflagellates has received comparatively little attention, yet they possess a distinct type of mitosis closely correlated with the

massive size and great number of the chromosomes. They furthermore show indications of a high degree of specialization along several lines. One of these is the development of a paradesmose, which reaches its maximum in *Noctiluca* with its "sphere," consisting of a mass of archoplasm containing the centrosome, which forms the axis of the karyokinetic figure. The rôle of the paradesmose (centrodesmose) in the dividing nucleus of these forms is one which still requires explanation and confirmation. The conflicting figures of Jollos (1910) and Borgert (1910) on this point in *Ceratium* show clearly the need of further investigation.

Another line of development is indicated in the large, distinctly marked chromosomes which, in some cases at least, do not entirely lose their individuality from one mitosis to another. In the living organism these are remarkably clear, appearing as moniliform threads of a clear, homogenous substance, and are evident in most of the individuals observed.

Figures of binary fission in the dinoflagellates are frequent in the literature, but a critical analysis of the various steps in the process has been made in only a few cases. Outside of the classical example of *Noctiluca,* only one member of the Gymnodinioidae, *Gyrodinium fucorum* (*Gymnodinium fucorum*) Jollos (1910), has thus far received such attention. The mitotic process has been outlined most fully in the thecate forms by Lauterborn (1895) in *Ceratium hirundinella* and in *Ceratium tripos* by Borgert (1910). The work of Jollos on *Gyrodinium fucorum,* though incomplete, combined with the scattered references to this subject that may be found in the literature, and our own observations on these forms, clearly indicates that the process is essentially the same for the majority, at least, of the Gymnodiniidae as that which has been described for the thecate forms. This conclusion is further strengthened by the identity in nuclear structure between the thecate and non-thecate dinoflagellates. As illustrative of the process of mitosis in this group we have therefore selected Borgert's work (1910) on *Ceratium tripos* var. *subsala.*

At the onset of division the ordinary spheroidal or ellipsoidal nucleus becomes elongated and, in some cases at least, the surrounding membrane is lost (fig. D, 1). The chromosomes lose their earlier parallel or subparallel arrangement and are found in a tangled skein or spireme, grouped in pairs (fig. D, 2). According to Borgert, this is the result of a longitudinal splitting of the individual threads. Lauterborn (1895) did not figure this stage in *Ceratium hirundinella,* nor did Jollos (1910) for *Gyrodinium fucorum, Ceratium tripos* or *C. fusus.* The work of both of these investigators left this stage still undetermined.

Following the spireme phase the chromosomes become arranged in an equatorial plate (fig. D, 3). In all cases the polar axis of the mitotic figure or spindle at this stage, as shown by the position of the chromosomes, lies in the short axis of the nucleus, necessitated doubtless by the great number of chromosomes. A definite spindle has not been figured by Borgert, Lauterborn, or

Jollos, though faint indications of it may be found in the cytoplasm beyond the ends of the chromosomes in some of Borgert's figures (fig. D, 4).

The next step in the process is the separation of the chromosomes into two groups (fig. D, 4) and the formation of the new daughter nuclei (figs. D, 5, 6). The chromosomes do not in this process lose their subparallel positions, but


Fig. D. Division of nucleus of *Ceratium tripos* var. *subsala* forma *typica*. After Borgert (1910, pl. 1, fig. 2; pl. 2, figs. 11–15). 1. Resting stage of nucleus. 2. Prophase with nucleus showing a segmented spireme with each thread double. 3. Equatorial plate stage. 4. Metaphase with division of the chromosomes. 5. Beginning of the anaphase. 6. Later anaphase. × 800.

this state seems to continue into the succeeding phases of nuclear development. In the dividing nuclei of *Cochlodinium elongatum* (pl. 4, fig. 45) the same appearance may be observed in the two newly formed daughter nuclei.

Jollos has figured for *Gyrodinium fucorum*, *Ceratium tripos*, and *C. fusus* a "centrodesmose" connecting two granules which seems to have a very problematical relation to the mitotic figure. This, as well as other obscure points, such as the exact method of division of the chromosomes and the presence of a spindle, still requires further investigation before they can be definitely settled.

The whole process of mitosis is of a relatively simple type which, correlated with the massive size and great number of chromosomes, makes it a distinctive one in the Flagellata. The evidence for the continuity of chromosomes from one division cycle to the next lies in the fact that the appearance of the daughter nuclei in the late telophase stage (fig. D, 6; pl. 4, fig. 45) is similar to that presented by the nuclei after final division of the body (fig. L, 2), and throughout

the ordinary trophozoite stage (pl. 8, fig. 83; pl. 10, fig. 114), without evidence of an intervening stage in which the moniliform chromatin threads or chromosomes are broken up.

Attention must be called to the appearance of the nucleus, as figured by Borgert, also by Lauterborn and Jollos, before the onset of division. The chromatin here lies imbedded as minute granules in the meshes of a reticulum that fills the entire nucleus, usually with one or more large nucleoli also present. This is in marked contrast to the appearance of the nucleus of the living organism. In the hundreds of individuals observed by us the nuclei presented a fairly uniform and characteristic appearance. In no instance has a network been visible and in only a very few cases have the granules been arranged in other than definite linear series. One of these is *Gyrodinium corallinum*, where a modification of the usual type of nucleus is present in the form of a surrounding alveolate zone (pl. 10, fig. 117). In a few cases the nuclei seemed homogenous, but usually they presented the distinct moniliform threads as shown in our figures. In a few instances these have been omitted in both the line drawings and the colored plates to avoid a too great mass of detail. With proper lighting conditions this structure can usually be demonstrated in the living organism.

The change of these linear threads to the minute granules enmeshed in a reticulum in the stained specimens may be due solely to the action of the fixative used in preserving the material. That a very great change takes place in protoplasm as well as nucleoplasm in the action of any chemical upon them is evident to any one working upon the living, in connection with stained, material of any protoplasmic body.

Chatton (1914*a*) has made perhaps one of the most important contributions to this question of nuclear structure in the dinoflagellates in his work on the parasitic forms. In *Blastodinium crassum* he figures (fig. E) details of nuclear structure, which clearly point to a greater complexity in the process of mitosis than has yet been demonstrated for the free-living dinoflagellates by any other investigator.

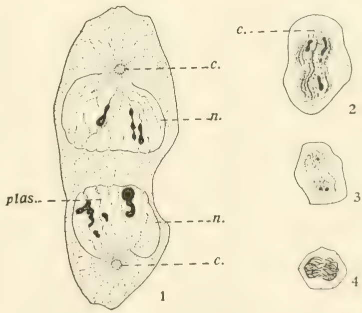


Fig. E. *Blastodinium crassum* Chatton. After Chatton (1914*a*, figs. 1–4). Abbreviations: *c.*, centrospheres; *n.*, nuclei; *plas.*, plasmodendrites. 1. Trophocyte in normal vegetative phase. 2. Sporocyte with remnants of the centrospheres still visible. 3. Sporocyte farther advanced with centrospheres completely obliterated. 4. Sporocyte of nearly last division stage. × ?

The appearance of the trophocyte, as Chatton has termed this peculiar, binucleated stage of the life cycle of *Blastodinium crassum* (fig. E, 1), represents a dinoflagellate in the late metaphase in which further development has come to

a standstill. At the opposite poles of the nuclei are large, conspicuous centrospheres with astral rays surrounding them (fig. E, 1, *c*). The relatively huge nuclei contain several nucleoli and are transversed by filaments, plasmodendrites (fig. E, 1, *plas.*), which are the remains of the nuclear spindle fibers formed by the division of the centrosphere or centrosome.

These peculiar structures are found in the sporocytes of all ages, but disappear with the maturity of the spore. In the last sporocyte divisions the centrospheres and achromatic figures disappear (figs. E, 2, 4) and a simple type of "Haplomitose" results.

In this still incomplete study of Chatton interesting questions concerning the complete stages of mitosis and nuclear development are raised, both in the parasitic and in the free-living forms. The difference between the two types may be due, as he suggests, to the influence of hypernutrition consequent on a parasitic mode of life within the digestive canal of pelagic copepods. A comparison of free-living and parasitic forms elsewhere among the Protozoa outside of the Sporozoa, where free-living forms are not found, does not suggest this as a probable solution. There are suggestions in some of Borgert's figures (1910, pl. 2, figs. 12–14) of an archoplasmic structure corresponding to spindle and polar regions. It may well be that further studies on these forms, with more critical cytological differentiation, will demonstrate the presence of such structures and reveal a closer similarity between the processes in the free-living and parasitic forms.

Pusules.—A well developed pusule apparatus is usually present in all the dinoflagellates. It consists essentially of a sacklike vacuole connected with the exterior by a slender canal opening into a flagellar pore. The fluid contained within it has a delicate rose or pale salmon pink color. The exact relations of the flagella and their blepharoplasts to the walls of the canal are uncertain. Their insertion seems to be a short distance below the opening of the pore. Two pusules are usually present, one opening anteriorly into the anterior flagellar pore, the other opening posteriorly into the posterior one. These two pusules may occasionally be united by a slender canal, forming a long channel opening at either end into a flagellar pore. In many species, particularly in the thecate forms, one or two branches or accessory pusules are formed as offshoots from the main collecting pusule. These are more or less temporary and not as constant in their occurrence as the main pusule.

In the thecate forms the pusules are usually relatively huge, often with accessory branches. Their size and their pink color combine to make them the most conspicuous features of many of the species. For this reason they attracted the attention of earlier biologists, and their structure and homologies were the subject of some speculation. Bütschli (1885) compared them to the contractile vacuoles of other better known Protozoa, and in this he was followed by Schütt (1895) in his comprehensive discussion of the subject. The latter investigator also pointed out the difference between the ordinary fluid vacuoles

that are usually present in the cytoplasm and the rather complicated pusule apparatus. In the latter he distinguished four or more parts, including a sack pusule, a collecting pusule, smaller daughter and accessory pusules in the surrounding cytoplasm, with a pusule canal extending to the periphery of the body from the main pusule. This entire structure he considered homologous with the contractile vacuole of the ciliates and rhizopods.

A superficial examination reveals a general similarity in appearance between the two structures. A closer examination, however, brings to light striking differences. Unlike contractile vacuoles, these pusules possess a distinct envelope or membrane, and contractions have never been observed.

This structure, moreover, has been shown by Kofoid's work (1909) on *Peridinium steini* to be connected directly with the intake of fluid into the body, and not, as might be expected from the function of similar organelles in the ciliates, as a collecting pusule for the discharge outward of fluids within the body. The actual process of filling up from the surrounding medium has been observed by us in some species of *Gymnodinium*, and in these cases did not occur gradually but with a sudden inrush that immediately inflated the pusule. The varying sizes and degree of development of these structures are dependent upon the periodicity of their functioning, and this evidently accounts for their presence in one individual and absence in another of the same species.

The process is essentially as follows: The fluid is taken in at the pores as a result of the activity of the flagella, particularly of the waves of contraction of the transverse flagellum, which tends to carry a current of water along the girdle to its proximal end and thence down the concavity of the ventral area, thus bathing both pores. There may be a continuous, gradual accumulation of fluid in the pusule or it may, by a sudden expansion, fill up with a rush. Vacuoles similar in color and refractive index to the pusules soon begin to accumulate in the plasma. In *Peridinium steini,* where this process was followed continuously for nearly five hours (Kofoid, 1909), minute vacuoles appeared in a layer around the sides of the pusule, followed shortly by larger vacuoles in the surrounding plasma. These collected in the peripheral zone, the outer border of which began to shrink away from the thecal wall, the space thus left vacant being filled with a fluid of the same rosy tinge as that found in the pusules and vacuoles. This fluid seems to be discharged from the surface, probably by osmosis.

Various stages of this process may be seen in our figures of the Gymnodinioidae, suggesting the similarity of their functioning with that of the pusules in the thecate forms. In *Gyrodinium capsulatum* the final stage of the process is in progress (pl. 5, fig. 54), with the vacuoles collected at the surface ready to discharge their contents into the surrounding water. In some cases the plasma is rather densely filled with these vacuoles (pl. 7, fig. 74), while in other cases the vacuoles are entirely absent. The huge size of the pusules in some individuals (pl. 5, fig. 57) and their entire absence in others suggests a periodicity

in their movements, though data on this point are entirely lacking. In some cases they are bilobed (pl. 10, fig. 108; pl. 12, fig. 132) and in others the two pores are connected by slender canals. The latter condition may possibly be a remnant of the ingestion area, by means of which a large food mass has been taken into the body. This condition is more frequently found in the more highly specialized forms, to wit, in *Cochlodinium, Pouchetia,* and *Erythropsis.*

The pusule apparatus of the dinoflagellates usually reaches its greatest development in the thecate forms, where daughter and accessory pusules are formed (Schütt, 1892; Kofoid, 1909), often of considerable complexity, and of relatively huge size. They occur in species possessing chromatophores, though their greatest development is reached where these organelles are entirely lacking. No solid contents have been observed in the pusules or in the vacuoles formed from them. The connection of these cell organs with the kind of nutrition existing in the absence of chromatophores and the fact that their greatest development exists in the forms whose theca of discrete plates would materially interfere with the ingestion of solid food strongly point to a saprophytic mode of nutrition in zones of decaying plankton. These facts also lead to the conclusion that the pusules, at least the anterior one, function as a cytopharynx for the intake of fluids and probably also of food particles into the body. The possibility of food vacuoles and food balls being formed in connection with the pusules is not excluded. The canal frequently found connecting the anterior and posterior pusules (pl. 7, fig. 76) suggests this possibility, since it probably represents the remnant of an ingestion area which has included the entire intercingular area of the sulcus. As has been pointed out in a previous paragraph, it is evident from the size of the ingested organisms sometimes found in the cytoplasm that the entire area of the intercingular sulcus must take part in the process of ingestion. The channel connecting the two pores, lying at the proximal and distal ends of this area respectively, would then probably persist as the internal remnant of its previous expansion, during which it functioned as the mouth of the organism.

OCELLI.—In the ocellus of the Pouchetiidae we find one of the most highly specialized organelles among the Protozoa. Among the dinoflagellates it is confined exclusively to this family, a similar structure not being present in any other group. The more primitive red eyespot, or stigma, of fresh-water *Gymnodinium* is hardly the equivalent of the ocellus.

The ocellate members of the Dinoflagellata were first observed by Pouchet, who figured several species as members of the genus *Gymnodinium* in a series of papers from 1883 to 1887. The "organe oculaire," as he termed this peculiar structure in the forms he observed, he described as a refractive, hyaline body with one end buried in a mass of dark pigment. He also advanced the suggestion that it probably functioned as a light-perceiving organ.

It was not, however, until the publication of Schütt's monograph (1895) that any adequate description or figures of the ocellus were presented. He

observed it in four species of *Pouchetia, P. juno, P. rosea, P. fusus,* and *P. compacta*, and also in two species of *Erythropsis, E. cochlea* and *E. cornuta,* though these two species he placed in the genus *Pouchetia*. Noting the advanced degree of development of this peculiar structure, he formed the genus *Pouchetia* for the ocellate dinoflagellates and placed therein all of the ocellate species described earlier by Pouchet.

Schütt distinguished two types of ocelli, one with brownish black pigment, as in *P. schuetti* (*P. rosea* Schütt), the other with reddish black pigment, as in *P. fusus.* The relation of these two colors, red and brown or black, in a single pigment mass he did not observe. The lens he described as composed of a single part, as in *P. cochlea,* or of several smaller moieties, as in *P. schuetti.*

Hertwig (1884) gave a fairly accurate account of the eyespot in *Erythropsis agilis*, describing its component parts as lens and pigment mass. Fauré-Fremiet in 1914 gave a fuller account of the structure of this organelle in the genus *Erythropsis* than had yet been attempted for any of the ocellate dinoflagellates.

The various points in which these descriptions differ from our own will be noted as we continue our discussion of this structure.

The ocellus of the Pouchetiidae is composed of two distinct parts, a refractive, hyaline, sometimes spherical lens (fig. RR, 1), and a surrounding pigment mass or melanosome (fig. RR, *mel.*). The lens or cristalline body of Pouchet varies in shape in the different species. In its more highly integrated form it is usually spheroidal in shape, clear and colorless and often asymmetrically laminated. This stage is reached in many of the species of the genus *Erythropsis* (pl. 12, figs. 129, 133), as well as in a few species of *Pouchetia* (pl. 11, fig. 118). In some cases, where distinct lamellae are not seen, its optical properties produce a play of colors not unlike that of a soap bubble (pl. 10, figs. 131, 134). In other species the shape may vary to an elongate form, more or less irregular in outline (pl. 6, fig. 61; pl. 11, fig. 126).

On cytolysis of the body the lens persists and when found free in the water it presents a colorless appearance. In the living organism it often reflects some tints of the surrounding cytoplasm (pl. 8, fig. 87) when partly buried within it, or it may show only a few of the prismatic colors when its position is protuberant above the cytoplasm, as in *Erythropsis pavillardi* and *E. cornuta* (pl. 12, figs. 133, 129).

The size and shape of the lens is not always easy to determine, since it is more or less covered by the melanosome. A certain amount of correlation between the size of the organism and the size of its ocellus is found in nearly all the members of the group. *Pouchetia parva*, one of the smallest species in the Pouchetiidae, has a length of 31$\mu$ for the body and a diameter of about 7$\mu$ for its ocellus. This is the smallest lens found in any species. The ratio between the size of the body and of the lens is greater here, however, than the ratio found in any other species. Thus in *Erythropsis cornuta* (fig. SS, 1) the lens has a diameter of 22$\mu$ while the body has a length of 101$\mu$. In the largest species of

the group, *Erythropsis cochlea* (fig. SS, 7), the diameter of the lens is only 16$\mu$ while the length of the body is 131$\mu$. In *Pouchetia polyphemus* (fig. OO, 11) the ratio between the length of body and that of the lens shows the greatest divergence, the former being about 104$\mu$ and the latter 8$\mu$. In *P. purpurescens* also this same divergence exists, though to a less extent, the length of the body being 58$\mu$ and that of the lens about 7.5$\mu$. In most of the other species, however, a closer correlation is found between the relative lengths of body and lens.

The size of the melanosome in relation to that of the lens is variable, due largely, perhaps, to the amoeboid character of the pigment. In most species it seems to be nearly equal to the lens in size, though probably not actually so, since the lens is usually partly buried within its substance. In a few species, notably in *Nematodinium torpedo* (fig. NN, 3), the melanosome has a relatively minute size. In *Erythropsis cornuta* (fig. RR, 1), on the other hand, the melanosome has a size equal to several times that of the lens.

The simplest form of the melanosome is seen in *Protopsis neapolitana* (pl. 9, fig. 96), where its relative size is also less than that of any other species except in *Nematodinium torpedo*. Here it is a loose aggregate of black pigment granules massed together at the anterior end of the lens, and apparently lacking the central core. A still looser aggregation of pigment is found in *Pouchetia poucheti* (pl. 11, fig. 125), but in this species the relative mass and size of the discrete particles of pigment have become much greater.

The melanosome throughout the entire group is mobile to the extent of moving freely around the lens, though no evidence of its movement to another part of the body has ever been observed. While under observation the pigment will spread over the face of the lens so that the latter is almost entirely obscured (pl. 12, fig. 130), or will recede until it embraces only the base of the lens (pl. 12, fig. 131). In some species amoeboid movements are noticeable, long pseudopodia being thrown out, sometimes around the lens (pl. 8, fig. 87), or away from the lens into the surrounding cytoplasm (pl. 11, figs. 121, 126; pl. 12, fig. 127). In many individuals while under observation this movement was continued so that no two camera sketches, made at short intervals of time, gave the same outlines for this remarkable organelle.

The center of the more highly integrated melanosome is occupied by a core of highly colored pigment (fig. RR, *core*). This is usually red, often brilliant in the more highly specialized forms (pl. 12, fig. 129) and light in tone in some of the others (pl. 11, figs. 118, 119). It apparently is not amoeboid, but seems to be connected with the base of the lens and forms the center or core around which the black pigment wraps itself. The character of its connection with the lens has not been clear in our material. At the time of cytolysis of the body the ocellus is usually the last part of the organism to disappear. The core then separates itself from both the lens and the black pigment and appears as a red subspheroidal body, which gradually wastes away without imparting its own tint to the surrounding water (figs. TT, 4–8). The black pigment also

rounds up into one or more spheroidal masses and undergoes the same fate. In one individual of *Erythropsis extrudens* observed the complete disappearance of the ocellus required twenty minutes from the time cytolysis began, the lens being the last part of the structure to dissolve.

Fauré-Fremiet (1914) has found that under the action of dilute acetic acid the pigment of the melanosome is transformed into a multitude of small globules of which part are brown and part are red. He evidently did not observe the red central core of the melanosome so prominent in some of our own forms (pl. 12, figs. 131, 134), though less noticeable in others (pl. 12, figs. 127, 129). The action of the acetic acid on the red pigment of the core explains the presence of the red granules in his figure of the melanosome thus treated. Schütt (1895) also failed to differentiate these two parts of the melanosome.

Various stages of integration of the ocellus are found within the group. The simplest form of the lens presented is that of separate, loosely aggregated, hyaline spheres, with scattered pigment granules partly surrounding them (pl. 11, fig. 125). From this simple condition a process of integration is clearly evident within the ocellate group, whereby the scattered pigment spherules are combined into a compact mass closely enveloping the base of the lens, with a correlated combination of separate spheres into a single, spheroidal lens, the greatest development of which is perhaps that of *Erythropsis cornuta* (pl. 12, fig. 129), or *E. pavillardi* (pl. 12, fig. 133). Various stages of this process may be seen in the Pouchetiidae, beginning probably with the genus *Protopsis* (fig. LL), though phases of the diffuse, less integrated types may also be found in *Pouchetia* (fig. PP, 4). In *Protopsis neapolitana* (fig. LL, 2) the melanosome is composed of relatively few pigment granules with a large spheroidal lens. A simpler condition is found in *P. nigra* (fig. LL, 1), where the lens also presents the diffuse type, being composed of several small spheroidal bodies.

In *Nematodinium partitum* the ocellus is diffuse in structure (fig. NN, 4), while in *N. torpedo* (fig. NN, 3) and *N. armatum* (fig. NN, 1) it presents a progressive integration both in the lens and in the melanosome.

Ocelli of the diffuse type are found in *Pouchetia poucheti* (fig. PP, 4) and *P. maxima* (fig. OO, 2), while most of the other species of that genus present a more or less well integrated type of structure. The extreme development of the amoeboid character of the melanosome is found in *P. subnigra* (fig. OO, 6) and in *P. alba* (fig. PP, 8), where diffuse strands of black pigment wander out through the cytoplasm. It is probable that the melanosome throughout the entire group possesses this characteristic property of amoeboid movement in varying degrees, as does the pigment found generally in the Gymnodinioidae.

The position of the ocellus is such as to receive the stimulus of light as the animal rotates in forward locomotion. It seems to be fairly constant in most of the members of the Pouchetiidae in its relation to the girdle and sulcus. In the genera *Protopsis*, *Nematodinium*, and *Pouchetia* it is usually found in the posterior half of the body, at the left of the intercingular sulcus and anterior

to the posterior junction of girdle and sulcus (figs. LL–PP). A few exceptions to this may be found. In *Nematodinium armatum* (figs. NN, 1, 2) it is located slightly posterior to the distal junction of the girdle and sulcus, as also in *N. partitum* (fig. NN, 4). In *Pouchetia purpurescens* (fig. OO, 7) the ocellus is located on the right side of the intercingular sulcus instead of the left when viewed from the ventral face. This species and *Protopsis neapolitana* (fig. LL, 2) are the only ones in which this organelle is thus located in the morphological right side of the body, instead of the left as in the other species. Owing to the torsion of the body and the varying positions from which it may be viewed, as well as its great transparency, this relation of ocellus and sulcus is often hard to determine. It is easily the most conspicuous part of the body and tends to obscure other structures lying near it. When the same organism is viewed at several angles, however, it is quite evident that the ocellus is situated on the morphologically left side of the body.

The orientation of the ocellus is also fairly constant throughout the group, with the lens anteriorly placed with respect to the melanosome. A few exceptions to this are found. In *Protopsis neapolitana* (fig. LL, 2) the melanosome is anterior, with the axis of the ocellus as a whole lying at an angle of about 45° with the main axis of the body. This is the only instance of this apparent anteroposterior reversal of the usual relations of the lens and melanosome to be found in the group.

A position in which the axis of the ocellus forms a right angle with the main axis of the body is more frequently met, as in the species of *Nematodinium* (fig. NN), *Pouchetia purpurescens,* and *P. maxima* (figs. OO, 7, 2). Nearly every gradation from this horizontal position of the axis to a vertical one is to be found among the species of *Pouchetia* (figs. OO, PP).

In the genus *Erythropsis* fewer variations are found. The ocellus is in all cases premedian and protuberant. One species only, *E. hispida* (fig. SS, 2), lacks the anteroposterior orientation of the ocellus to any marked degree. Here the two structures lie side by side, with the axis passing through both parts, thus taking a horizontal position. In the remaining species the ocellus is directed anteriorly. In *E. extrudens* (fig. SS, 11) the amoeboid melanosome at times nearly covers the lens, thus obscuring these relations. In the contracted state, however, the axis showed only a small change from a vertical position (fig. TT, 3).

Of the finer structure and constitution of the ocellus very little indeed is known. Fauré-Fremiet (1914) found that the lens was not acted upon by solvents for oil, such as alcohol and acetone. In alcoholic solution of iodine it became yellow. In our own material we found that it is the last part of the body to disappear in cytolysis, twenty minutes being required in one case for its dissolution in sea water.

The melanosome, at least the part outside of the core, is evidently similar in its constitution to the pigment that is frequently met with in other parts of the body. This is most clearly seen in the diffuse type of melanosome where

the pigment may be more or less broken up and scattered through the cytoplasm (pl. 11, figs. 121, 125; pl. 8, fig. 84). Its wandering movements are also characteristic of cytoplasmic pigment.

This connection between the pigment of the melanosome and the pigment scattered through the cytoplasm receives some confirmation in observations made by Fauré-Fremiet (1914) on *Erythropsis pavillardi*. The cytoplasm of the form he was working with was of diffuse rose color. Upon the addition of dilute acetone or weak acetic acid to the organism the color was concentrated in clusters of small red globules. The action of acetic acid on the melanosome caused its breaking up into small red and brown granules, belonging respectively to the outer dark pigment and to the core. The red granules presented a similar appearance to that of the "erythrosomes" or precipitated color of the cytoplasm.

Fauré-Fremiet's observations also indicate that the pigment composing the core of the melanosome is similar to that found in the cytoplasm. Thus far we have found no evidence in our own work to show that it possesses the mobility characteristic of the outer part of the melanosome. At the time of cytolysis it separates from the melanin as a spheroidal mass which may break up into two parts (fig. TT, 7). Under the action of the sea water it slowly dissolves, as does the remainder of the ocellus.

The behavior of this organelle at the time of division is totally unknown. In *Protopsis ochrea* (fig. LL, 4) Wright (1907) has figured a division stage in which the separation of the two zooids has not yet taken place. The ocellus as well as the girdles are fully formed in both daughter organisms. One large body is present in the cytoplasm, but whether this is the still undivided nucleus he does not state. It is probably a vacuole, as this stage of formation of the anatomical features of the body would indicate the completion of division of the nucleus. No hint is given as to the mode of formation of the ocelli. Division stages of the ocellate dinoflagellates have been entirely absent from our own material unfortunately, hence we can throw no light upon this subject.

The function of this remarkable addition to the structural characteristics of these flagellates is problematical. The reactions of these organisms to light and other stimuli are almost entirely unknown, due to the rarity of the organisms and to the difficulties of preserving them under conditions suitable for experimental observation. This organelle is apparently structurally adapted for and may be functionally efficient as a light-perceiving organ, though whether actually so remains to be determined by experiment.

Nematocysts.—Of all the organelles of the dinoflagellates two stand out distinctly as metazoan in their type of structure. These are the nematocysts and the ocelli. The latter structures are peculiar to the dinoflagellates alone, while the former have a wider distribution in the Protozoa, being found throughout the Cnidosporidia and in at least one species in the Ciliata, *Frontonia leucas*. In the Dinoflagellata they are found in two genera, *Polykrikos* and *Nematodinium* (*Pouchetia armata* Dogiel).

These organelles were first figured by Bütschli (1873) as "Nesselkapseln," a term also used by Bergh (1881) in describing the same structures in *Polykrikos auricularia* (*P. schwartzi*). Pouchet (1887) figured them as nematocysts without, however, giving the details of their structure, as both Bütschli and Bergh had done. Fauré-Fremiet (1913*a*, *b*) was the first one to attempt a more critical analysis of the origin and nature of these peculiar organelles. He was followed by Chatton (1914*c*), who figured an elaborate stage of cyclical development, markedly different from that outlined by Fauré-Fremiet. A further analysis of these schemes of development will be given after the minute structure of these organelles has been described.

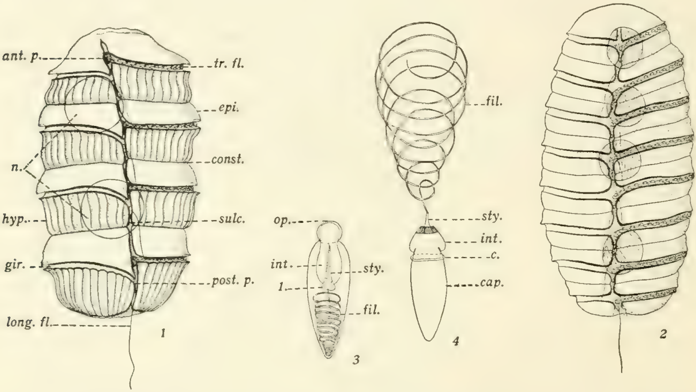


Fig. F. *Polykrikos* Bütschli, and its nematocysts. 1. *P. kofoidi* (Kofoid). × 500. Individual of four zooids. After Kofoid (1907). 2. Nematocyst. × 1550. 3. Exploded nematocyst. × 1148. 4. *P. schwartzi* Bütschli. × 500. Abbreviations: *ant. p.*, anterior pore; *cap.*, head of nematocyst; *epi.*, epicone; *fil.*, filament; *gir.*, girdle; *hyp.*, hypocone; *long. fl.*, longitudinal flagella; *n.*, nuclei; *post. p.*, posterior pore; *sty.*, stylet; *sulc.*, sulcus; *tr. fl.*, transverse flagella.

The structure of the nematocysts of both *Polykrikos* and *Nematodinium* is practically identical. The matured organ is found lying naked in the plasma (pl. 11, fig. 122), without any special plasmatic membrane or structure surrounding it, or any differentiated protoplasmic nidus in which it originates, or any external plasmatic structure which might function as a cnidocil. The position of the nematocysts in the body of the dinoflagellate is not constant. They may be found in all parts, though perhaps most frequently in the right half of the body. Their orientation is also subject to great variations, with no apparent relation to the surface of the body. Chatton (1914*c*) found that the greater number were oriented with the pole of devagination turned towards the surface of the body. In our own material this orientation seems no more

frequent than positions in which the pole of devagination is turned away from the surface.

The matured organ has a length varying from $5\mu$ to $22\mu$ in the two genera. In *Polykrikos* the average length is slightly greater than in the smaller species of *Nematodinium*. In two species, *N. torpedo* and *N. partitum*, of the latter genus the nematocysts range in length from $5\mu$ to $8\mu$, while those of *N. armatum*, with its much greater size of body, range from $14\mu$ to $22\mu$, a size comparable with that of the organelles in *Polykrikos*.

The shape of the nematocyst is slender oval (fig. F, 2), surmounted by a caplike portion at the broader end. It consists of an external capsule (*cap.*) of considerable rigidity, which Chatton regards as chitinous in its nature. Beginning at the base of the caplike portion in the interior of the capsule is an introverted sacklike extension (*int.*), which may reach to near the middle of the capsule. This is continuous with the sides of the capsule as may be seen in the exploded nematocyst (fig. F, 3, *int.*), in which this portion is everted and thrown forward. To this structure Chatton has given the name ampulla (ampoule).

Arising from the bottom of the interior of the introvert or ampulla is a small cone-shaped thickening from the apex of which a slender stylet (*sty.*) extends forward with a length nearly equal to that of the introvert, ending free in the cavity. At the base of the introvert, opposite the origin of the stylet, the thickening is continued into two lobelike bodies (*l.*) from the point of intersection of which springs a slender filament (*fil.*) of considerable length, probably continuous with the walls of the capsule, the spiral coils of which fill the posterior portion of the cavity. The exact relation of this filament to the stylet is hard to determine. In the figures of both Bütschli and Bergh the stylet functions as the base of the filament when the latter has been discharged from the capsule. In Fauré-Fremiet's figure the stylet remains within the introvert, or rather is thrown backward after the discharge of the nematocyst. Chatton, however, finds that the rôle of the stylet is that of an organ for piercing the operculum at the time of discharge and is not directly connected with the filament, which passes through the thickened portion of the introvert at the base of the stylet (fig. G), and is thrown off after the discharge of the nematocyst.

At the anterior end, surmounting the caplike head, is a minute operculum (*oper.*) which marks the point of emergence of the stylet in the discharge of the nematocyst.

No evidence is forthcoming regarding the normal discharge of these organelles. When the body wall is ruptured and the nematocysts come in contact with the sea water the discharge is usually instantaneous in the case of the fully matured organelles. The addition of weak acetic acid, formalin or alcohol will also cause a discharge. This process requires but a small fraction of a second for its accomplishment, hence the details of it are difficult to observe and conflicting reports as to the manner in which it takes place have resulted.

Fauré-Fremiet (1913) described the discharge of the nematocysts as a rupture of the extreme anterior end of the capsule, with an eversion of the introvert and a rapid unrolling of the filament. Chatton has given a much fuller description of this process and one that differs in some essential details from our own. According to his interpretation, the filament is not an integral part of the structure of the nematocyst, continuous at its base with the walls of the introvert, but is a distinct structure. A the time of explosion the introvert is forced outward, following a rupture of the extreme anterior end of the head of the nematocyst, and the filament is thrown out as a simple unrolling. He figures no process at its posterior end by which its entire escape from the nematocyst may be prevented.

In these structures, which are similar in practically every detail to the nematocysts of the Coelenterata (fig. H, 3), a similarity in their explosive action is to be expected. That this similarity exists would seem to be borne out by certain features in their structure and in the appearance of the exploded organelle. In the hydroids additional structures, as short spines, are often present within the coiled filament. In the exploded cell these are found on the outer part of the filament, leaving no doubt as to the fact of its eversion as a tube at the time of discharge (fig. H, 4). In the dinoflagellates no such structures exist, hence, as the actual process cannot be followed with the eye, the manner of it must be inferred by analogy and by the appearances of the nematocysts both before and after discharge.

Our own interpretation of the explosion of the nematocysts is as follows: Contact of the anterior end or head of the nematocyst with an appropriate stimulus, such as sea water, causes its rupture with explosive abruptness, and the introvert is thrown out. The ruptured membrane remains like a collar (fig. F, 3) around the basal portion of the introvert in its new position (fig. F, 3, *int.*). As this latter structure is everted the stylet and thickened basal portion (*sty.*) occupy the extreme anterior end of the nematocyst. Simultaneously with this outward projection of the introvert the filament is thrown out (fig. F, 3, *fil.*) as an everted long slender tube. In this position it is found to be continuous with the anterior end of the nematocyst (fig. F, 3).

The filament is a slender, double-contoured thread, the tubular nature of which is hard to demonstrate. That this is its structure would seem evident from its appearance at the time of explosion of the nematocyst, and by analogy with similar organs in the Cnidosporidia (Doflein, 1911) and in the hydroids (Toppe, 1910) (fig. H). After explosion it is connected and apparently continuous with the walls of the nematocyst at the extreme anterior end of this structure. This is also shown in Chatton's figures, one of which is reproduced in our figure G, 10.

As has already been pointed out, Chatton does not figure any mechanism by means of which the filament retains its relation with the nematocyst after its explosion. A slender thread which has no organic connection with the

capsule would be thrown beyond its confines completely at the time of explosion, which does not seem to be the case in any of Chatton's figures. On the contrary, the extreme posterior end of the filament remains connected with the extreme anterior end of the nematocyst in all cases (fig. G, 10), a fact that would point to an intimate relation between the two structures. It seems probable, therefore, that the filament in the nematocysts of the dinoflagellates has a tubelike structure and is everted at the time of discharge of the nematocyst, as in the case of the Cnidosporidia and Coelenterata (figs. H, 4, 5).

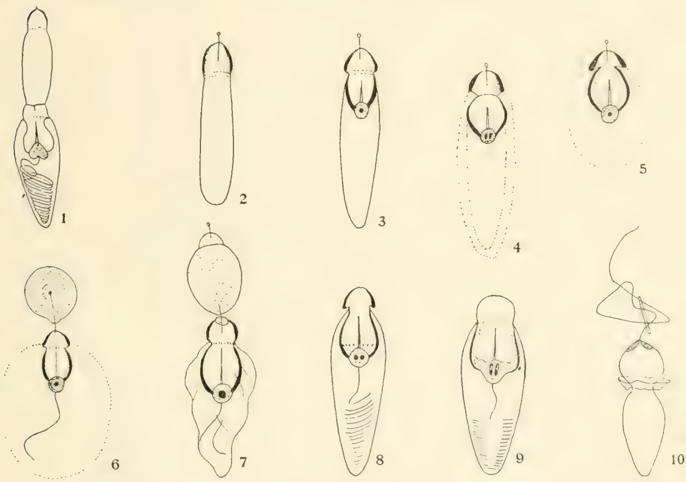


Fig. G. Development of the nematocysts of *Polykrikos*. After Chatton (1914*c*, pl. 9, figs. 2, 4–7, 10–12, text figs. 6, 7). 1. Mature nematocyst with its cnidoplaste attached. 2. Cnidoplaste detached with differentiation beginning at anterior end. 3. Cnidoplaste with the introvert and stylet developing. 4. Body of cnidoplaste dissolving, leaving vacuole around it. 5. Further stage of the same, changing of cnidoplaste into cnidogene. 6. Cnidogene stage, introvert and flagellum suspended in vacuole, sphere forming anteriorly which is future cnidoplaste. 7. Further development of cnidogene. Body of nematocyst forming in vacuole. 8. Cnidogene developed into young nematocyst. 9. Further development of the same. 10. Exploded nematocyst with stylet thrown off. × ?

Chatton figures cases in which the nematocysts have been caught, as it were, in the act of exploding, with the filament partly within and partly without the capsule. This appearance is not inconsistent with our explanation of the process as that of an eversion of a slender tube, as may be seen by partly withdrawing the finger of a glove that has been turned inward. A point will be reached where the finger extends some distance on each side of its point of insertion, as does the filament in his figures (1914*c*).

Another point somewhat unconvincing in Chatton's work is the rôle he has attributed to the stylet. This he figures as a slender rod, slightly conical, with the base wider than the apex (fig. G). This shape is constant in all his figures showing the stylet in the still unexploded nematocyst. After the explosion has taken place its position in the center of the thickened portion of the introvert is occupied by the filament. Near at hand, as though pushed out of position by the filament, is a rod (fig. G, 10) differing in length and thickness from the stylets which he has figured in the unexploded nematocysts. In our own material (fig. F) the base of the filament after it has been discharged shows a slight enlargement comparable with the appearance of the stylet in the unexploded capsule. It seems probable, therefore, that here, as in the nematocysts of the coelenterates, the stylet functions as the base of the extruded filament.

The development of these interesting organelles has also proved to be a puzzling question, the solution of which has been greatly advanced by the researches of Chatton (1914*c*). Fauré-Fremiet (1913) has offered a scheme of development of the nematocysts from the small refractive granules common in the cytoplasm. He presents no stages, however, between the small round granules and the elongate body of the young nematocyst. These refractive granules and small globules are common throughout the dinoflagellates generally, and since nematocysts are not common elsewhere more evidence is required before they can be considered part of the development of these peculiar organs.

Chatton (1914*c*) offers another type of development which is cyclical in character and of a considerable degree of complexity (fig. G). It consists of three distinct stages, the first of which is the "cnidoplaste" (figs. G, 1–5), which appears to arise from an organ resembling the centrosome. The cnidoplast arises by a process of "autogenese" from the mature nematocyst. Part of this process is shown in figures G, 6, 7, in the body forming at the anterior end of the developing nematocyst. The cnidoplast is not enclosed in a chitinous capsule and deliquesces readily in sea water. It goes through a process of development by which the anterior end is transformed into a new structure, the "cnidogene," and the remainder of the body dissolves, its place being occupied by a large vacuole (figs. G, 2–6). The cnidogene gradually develops into the finished nematocyst. Chitinization of the body of the future nematocyst or cnidocyst takes place in this vacuole while further development of the internal structure of the capsule progresses (figs. G, 7–9). This results in the production of the filament and the introvert or ampulla, and the cnidogene becomes the mature nematocyst (fig. G, 9).

The number of mature nematocysts in the body of both *Polykrikos* and *Nematodinium* varies in different individuals. In our own material of *Polykrikos* the number has run from one or two less than the number of zooids to twice the number of zooids of the body. Chatton has found that variations may exist in the number of young forms or "cnidoplastes" (fig. G, 2), and also in the number of mature nematocysts. In the secondary stage of their

development, the "cnidogene" (fig. G, 6), he states, however, that the number is constant and equal to the number of zooids of the body, and also that they are metamerically arranged. Thus he figures (1910*c*, pl. 9, fig. 1) an individual of eight zooids, each one of which contains a single "cnidogene," centrally located and oriented at an angle of about 45° from the longitudinal. The excess of cnidoplasts formed are ejected from the body or dissolution takes place *in situ*.

This metamerism of the nematocysts is not shown in our own material nor in the figures of other investigators, including Chatton's figures of the mature organelles. Its existence is thus apparently limited to this single stage of its development.

It is thus seen that the exact origin of these structures still remains a doubtful point, as does also their fate after the completion of the development of a new set of organelles in the body. Chatton has suggested that the old nematocysts are dissolved in the cytoplasm, and in proof of this figures a colored refractive body frequently seen by him in *Polykrikos* (1910*c*, fig. 15, pl. 9). A comparison of his figure with some of the cell inclusions in other species of the Gymnodinioidae as shown in our own material (pl. 4, fig. 46; pl. 5, fig. 52) shows that a closely similar structure is frequently present in other forms where nematocysts do not occur, and lessens the probability of this being a disintegrative phase of these organelles.

## CHAPTER III

# GENERAL MORPHOLOGY: CYTOPLASMIC DIFFERENTIATION, COLORATION, SURFACE DIFFERENTIATION

Cytoplasmic Differentiation.—The tribe Gymnodinioidae presents both extremes of cytoplasmic complexity found within the Flagellata, its lower forms having the simplicity of structure found in the lower flagellates, and its more highly specialized ones being exceeded in complexity only by the Trichonymphidae. In most of the species no distinct ectoplasmic differentiation can be detected, beyond the presence of a thin periplast surrounding the body (figs. X, CC). Varying degrees of differentiation leading up from this simple type may be found with its highest development shown in the subgenus *Pachydinium* of the genus *Gymnodinium* (fig. AA).

A distinct ectoplasm is present in this subgenus showing a degree of specialization reached elsewhere only by the Ciliata. This, as appears in *Gymnodinium pachydermatum* (fig. AA, 5), consists of a relatively wide, clear, homogeneous, double-contoured zone surrounding the endoplasm. Superimposed upon this zone is an outer, alveolar layer, somewhat wider than the inner zone of homogenous ectoplasm. The outer facets of the alveoli are rounded and give to the surface of the body a roughened, irregular contour. The alveoli are filled with a clear homogeneous fluid of the same consistency as that found in the inner zone of ectoplasm.

Correlated with this specialization of the ectoplasm is a relative complexity of endoplasm shown in the presence of radial rodlets, vacuoles, oil droplets and refractive granules. In some species the radial rodlets seem to occupy definite places in the plasma and are probably intimately related to the metabolic activity of the organism. They may be lacking in a few individuals and present in others of the same species. Their usual location is near the anterior pore and leading out towards the periphery of the body. They may sometimes be observed streaming out from the pusule (fig. V).

In many other species showing a lack of ectoplasmic differentiation a zone of short rodlets is often present in the peripheral region, closely packed together and at right angles to the surface (fig. CC, 7). In end view these appear like small vacuoles. These apparently have the same structure and greenish color as the longer, centrally located ones, and evidently subserve the same or similar purposes in the life economy of the organism. They are probably connected with a saprophytic type of nutrition, since they are never present in forms possessing chromatophores. They are also absent generally in the more highly specialized members of the Gymnodinioidae, such as *Cochlodinium*, and the Pouchetiidae, where nutrition is probably holozoic throughout.

These rodlets or rhabdosomes, as they have been called by Schütt (1895), are constantly present in the different individuals of many species, while in other species they may be present in a few individuals and absent in others. With the cytolysis of the body these rodlets melt away as do the fluid-filled vacuoles, indicating a similarity in their structure. We have, therefore, confined the term rhabdosome to those structures which have a greater permanency, as in the long slender rhabdosomes constantly present in the genus *Torodinium* (fig. II), and which do not deliquesce so readily as do the ordinary vacuoles of the cytoplasm.

The endoplasm is usually visibly granular, but in the genus *Erythropsis* and in a few species in other genera this granular appearance is lacking, the body presenting a hyaline, almost glassy texture that persists in *Erythropsis* until cytolysis of the body occurs.

Coloration.—The pelagic dinoflagellates are remarkable for their diversity of coloration and for a brilliancy and delicacy of tone which give to the minute transparent body a beauty that is almost impossible of analysis and equally difficult to reproduce. In comparatively few species is the color confined to a single tint except in those forms having chromatophores or colored pigment. The usual condition shows a background of soft pearl grey shot through with one dominant color, intermingled with broken flashes of one, often two or more, contrasting colors, the entire combination producing a rich effect impossible of adequate reproduction.

The color may be resident in chromatophores (pl. 1, figs. 1, 4), yellow, yellow ochre or greenish, or in pigment granules (pl. 6, figs. 65, 67, 69), or it may by diffusion be a component part of the cytoplasm itself, with no evidence whatever of localization in even minute particles (pl. 6, figs. 63, 68). A relatively greater number of thecate forms than naked dinoflagellates possess chromatophores. In case of naked dinoflagellates the chromatophores are confined to the simpler, more generalized species, namely, *Amphidinium* (fig. U) and the lower forms of *Gymnodinium* (fig. X) and *Gyrodinium* (fig. CC). In the more highly specialized groups of the Gymnodiniioidae they are almost entirely absent, as in *Pouchetia* (pl. 11) and *Erythropsis* (pl. 12).

Nearly the whole range of colors of the spectrum are to be found within the species of the different members of the Gymnodiniidae. It is noteworthy also that a certain amount of correlation may be found in the group between the coloration and the amount of specialization attained within the group. In *Amphidinium* the predominating colors are green and yellow (pl. 1, figs. 1, 4, 11), correlated with a relatively greater number of chromatophore-bearing forms. The colors of the red end of the spectrum are entirely unknown in this genus.

In the genus *Gymnodinium* its most specialized species, such as *G. pachydermatum, G. dogieli,* and *G. amphora* (pl. 3, figs. 32, 34, 26), show a type of differentiation which throws them outside the line of evolution which produces

the higher or more advanced genera, these having evidently come from the simpler, more generalized, but rather highly colored species, as *G. violescens* (pl. 6, fig. 69), *G. rubricauda,* and *G. rubrum* (pl. 8, figs. 88, 86).

In the genus *Gyrodinium* the type of structural specialization has not gone beyond that attained by the genus *Cochlodinium.* It has no species which show a great degree of specialization peculiar to that genus alone, such a specialization as is found in some species of the genus *Gymnodinium.* Some of its most highly colored species, as *Gyrodinium virgatum* (pl. 10, fig. 112), are among its most advanced species leading on to the next genus, *Cochlodinium.*

In the genus *Cochlodinium,* as in *Gymnodinium,* the species showing the most brilliant colors, especially those near the red end of the spectrum, fall within its more generalized group, that is, without the extreme torsion of the body. These species are *C. miniatum* (pl. 10, fig. 107), which is closely allied to *Gyrodinium, Cochlodinium constrictum,* and *C. rosaceum* (pl. 8, fig. 85), the latter species probably representing the closest approach to the type of structure of the Pouchetiidae found within the genus.

In the Pouchetiidae a yellow color is only rarely met with, the predominating tones being those near the red end of the spectrum and in the green section (pl. 8, figs. 84, 87, 89, 90; pl. 11), combined with melanin appearing almost for the first time in the ocellus of this family. In the most highly specialized member of the family, *Erythropsis,* yellow is unknown, while red pigment in some form is found in nearly every species in combination with melanin in the ocellus (pl. 12), or localized in the cytoplasm as in one species, *E. scarlatina* (pl. 12, fig. 128).

The presence of melanin within the group, while less common, also bears the same relation to the amount of specialization, that is, it is found within the line of advance from the simpler to the more complex members of the group. It is present in *Gyrodinium spumantia* (pl. 7, fig. 72) and *Cochlodinium atromaculatum* (pl. 7, fig. 71) alone among the members of the family Gymnodiniidae. In the family Pouchetiidae melanin is found in all the species, occasionally scattered through the cytoplasm (pl. 11, fig. 119), but more commonly confined to the melanosome (pl. 11, figs. 118, 122).

It thus appears that an advance in specialization within the group as a whole runs from the simpler types, with a predominant yellow or green color, as in *Amphidinium,* through the more brilliantly colored species of *Gymnodinium, Gyrodinium,* and *Cochlodinium,* to the Pouchetiidae, with the predominating colors in most of the species near the red end of the spectrum. Specialization within the genus, however, below the Pouchetiidae, is usually found to occur in those species which are not highly colored, where this specialization leads to one side of the main advance from one genus to the next, as in *Gymnodinium pachydermatum* and its allied species.

Within the Pouchetiidae, however, the progressive structural specialization within the group leads from the species with faintly tinged bluish green to the

red and black colors, the advance being shown in the increasing specialization of the ocellus, sulcus, and girdle. In the genus *Pouchetia* the species displaying some tones of red, as *P. compacta, P. voracis, P. rubescens* (pl. 8, figs. 89, 90), and *P. maculata*, with the group of purplish species, *P. purpurata, P. purpurescens*, and *P. schuetti*, are its most highly specialized members, as shown in the degree of integration of the ocellus and the complexity of the girdle and sulcus.

A few exceptions to this general tendency may be found, as in *P. violescens* (pl. 11, fig. 118) and *P. juno*, which are also highly specialized species in structure, though not in color. A few exceptions also may be found in the other genera. The preponderance of evidence, however, suggests that these lines of structural evolution are, in the main, correlated with progressive movement in coloration towards the red end of the spectrum throughout the larger groups of the Gymnodinioidae.

The fresh-water species of the group, confined to the genera *Amphidinium, Gymnodinium*, and *Gyrodinium*, are markedly less brilliant in their color than are the pelagic forms. They are colorless, as in *Gymnodinium helveticum* and *Gyrodinium hyalinum*, or with dull green or yellow ochre chromatophores, as in most of the other species found in that habitat. The only apparent exception to this conclusion is found in the presence of a minute red eyespot in the midventral sulcal area. This may be homologous with the pigment formation common in the pelagic species, but not with the ocellus as a whole, though it may be represented in the red core of the latter organ. It is rather a structure comparable to the eyespot or stigma of *Euglena* and other fresh-water flagellates.

Pigment in some form is common in many of the members of the Gymnodinioidae, and frequently becomes the most conspicuous feature of the organism, as in *Gymnodinium lineopunicum* (pl. 6, fig. 65), with its markedly motile pomegranate purple pigment. This pigment, as frequently seen in other species also, is almost constantly changing its position under apparently normal conditions, with the organism still active and no indications of the approach of cytolysis. So constantly was this change taking place in the individual shown in plate 6, figure 65, that a complete camera sketch of its appearance at one time could not be obtained.

A more striking instance of the motility of pigment in these forms is shown in *Gyrodinium ochraceum* (pl. 7, figs. 76, 82). In examining a number of individuals of this species a great difference was noted in the pigment formation among them. In some specimens the pigment would be diffused uniformly throughout the body in minute grains. In others these would be localized into larger granules, as in figure 76. Still others would exhibit various stages between that condition and the band of pigment wound spirally about the body (pl. 7, fig. 82). These appearances were puzzling in the extreme. It was not, however, until a single individual was held under observation for a considerable length of time that an explanation was found.

When first observed this individual presented an appearance like that shown in figure 76, with the pigment in scattered granules. In a short time a change began to take place, the pigment moving slowly into the region of the girdle and collecting into a wide mass or band which extended some distance on both sides of the girdle (pl. 7, fig. 82). Though normally pigment occupies a position close to the periphery of the body, yet this band formation took place inside of the girdle without extending into the lips of the girdle, which were clear. The remainder of the cytoplasm was apparently free from pigment also. Soon after this formation was completed further changes began. Small nodules appeared along the margin of the band, like outpushings from the main mass. These were pinched off and began to move out into the cytoplasm. This process continued until the entire band had become dissipated, the granules moving away until at the end of the period of observation the individual again presented the same appearance as when first noted (pl. 7, fig. 76).

Indications of this same motility of the pigment are to be seen in the red pigment in *Gyrodinium corallinum* (pl. 10, fig. 117). The position of this in the cytoplasm varies greatly in different individuals as well as in successive periods of time in the same specimen. One peculiarity of the movement of coloring matter or pigment in species which have a striate surface may be observed in this form. This is the marked tendency of such material to follow the lines of striae on the surface, where it may collect in small granules or become massed in long bands. *Gyrodinium fulvum* (pl. 7, fig. 70) and more strikingly, *G. virgatum* (pl. 10, fig. 112), exhibit this same peculiarity.

Another marked feature of the behavior of pigment in these forms is the tendency to collect in the epicone, especially near the apex, leaving the hypocone relatively free, though usually not entirely so, from the colored granules. In *Gyrodinium maculatum* (pl. 6, fig. 62) the abundant, violet-colored pigment is densely massed in the epicone, so that under the low powers of the microscope this part of the body appears almost black, while the smaller granules in the hypocone are sufficient only to give it a violet tinge.

A few exceptions to this general rule are to be met with. In *Gyrodinium postmaculatum* (pl. 6, fig. 64) the color is massed at the antapical end, leaving the anterior end of the body free from agglomerated masses of color. The same condition is found in *G. rubricaudatum* (pl. 10, fig. 116). In *Erythropsis scarlatina* (pl. 12, fig. 128) still another modification is found. In the anterior part of the organism the pigment is confined more or less closely to the periphery of the body, while in the centroposterior part it occupies the interior of the body with amoeboid ramifications extending through the cytoplasm.

It is not uncommon to find, on the approach of cytolysis, that the color which has before been completely diffused through the cytoplasm becomes localized or condensed into granules, the erythrosomes of Fauré-Fremiet (1914). This same condition may be produced by the addition of dilute acetic acid, as Fauré-Fremiet has shown for the rose-colored specimen of *Erythropsis pavillardi*.

This appearance may also be produced by lack of oxygen or other adverse conditions consequent on a small supply of fluid under a cover slip during microscopical examination. In *Peridinium crassipes* the bright coral red color may be observed in its condensation under the microscope. This will continue until the cytoplasm is colorless and filled with red balls of a considerable size. The addition of fresh sea water to the surrounding medium will, in some cases where the adverse conditions have not killed the organism, result in a diffusion of the color with an almost complete disappearance of the red granules in the cytoplasm.

In the case of *Gyrodinium ochraceum*, recorded above, the condensation and subsequent diffusion of the pigment is evidently not caused by adverse conditions in the surrounding medium since individuals showing all stages of the process may be found in the same haul. It may be due to physiological conditions in the organism itself or to the reacton to stimuli resulting from its own activities or to light, or other factors of its surroundings. The relatively rapid changes under the microscope are probably due to the progressive changes taking place in the surrounding medium.

The localization of pigments near the girdle, sulcus, longitudinal striae and at the apices is suggestive that internal oxidation processes resulting from contraction, and from other internal responses to stimuli, are potent factors in determining the origin, location, and movements of these products of the living substance.

Surface Differentiation.—The typical naked dinoflagellate differs but little, if at all, in its ectoplasmic structure from the ordinary flagellate. A differentiated ectoplasm, as distinct from the endoplasm, is only rarely met with beyond the production of a thin periplast covering the body. This is thin and elastic and allows for considerable metabolic changes of the body form (fig. A), yet is firm enough to preserve a remarkable similarity in shape throughout the individuals of any given species. To such changes some areas of the body are more susceptible than others, as in the antapical region and the posteroventral surface near the sulcus (fig. T). These areas of great susceptibility are undoubtedly correlated with the function of these portions of the body, the antapical region serving as a vent for the ejection of unused or waste material from the body and the sulcus for the ingestion of food.

The periplast may be marked by lines, ridges or furrows of varying degrees of development. Striae are usually confined to the outermost border of the periplast, but occasionally may be deeper seated and may be indicative of a fundamental organization of the protoplasm, as shown by the linear arrangement of pigment (figs. DD, 9, 21). These surface markings are in all cases longitudinal, extending from the girdle to the apices, diminishing in number near the poles and often fading out entirely in the apical regions. Different kinds of surface markings may be present in one species, as furrows and linear lines or dots (fig. W, 3).

In the tribe Peridinioidae, as in the Prorocentridae, the surface is still further elaborated by the development of a theca of discrete plates, often of a perfection of form and finish and of a beauty of design surpassed by no other similar group of structures. This exoskeleton exhibits a tendency to show longitudinal linear markings not unlike the linear striae of the periplast of the unarmored dinoflagellates in number, location, and distribution.

CHAPTER IV

# PHYSIOLOGY: "RED WATER," NUTRITION, REACTIONS TO STIMULI, LUMINESCENCE

In the Protozoa we find all life processes reduced to their simplest expression. This makes for simplicity of function, but since these functions are all carried on within the compass of a single microscopic cell it often conduces also to complexity of organization. As not infrequently happens, a single group of organisms may present a wide range of structural differentiations, with consequent modifications of physiological activities.

This is particularly true of the Flagellata, which present the elementary characteristics of both plant and animal organization. The dividing line between these two types of organization and the resulting physiological activities which mark the plant and animal kingdoms cannot be drawn with certainty between orders, families, genera or even species among certain Protozoa, since in some groups even related species may respectively exhibit the two types of organization. Such a group is the Dinoflagellata. In the members of this group we find forms of the simplest type of organization, as well as some which exhibit the highest degree of specialization, in some features, to be found within the Protozoa, and we find also types of nutrition ranging from the typically plant method through saprophytic to the typically animal mode of food-getting. This condition makes these organisms of peculiar interest to the biologist because of this intimate interrelation of such diverse functions.

The physiological activities of this group have, however, received but little attention. A few scattered references to the subject may be found in the literature, but the data given on such constituent parts of the body as starch grains, amyloid bodies, etc., have usually not been based on definite experimentation and therefore are inconclusive. No work has thus far been done along this line by the present authors, hence this subject can only be touched upon lightly, with tentative conclusions which must await definite experimentation for confirmation.

The dinoflagellates probably rank next to the diatoms in their abundance in the sea and in their importance as a food supply for the smaller plankton life which feeds upon the great oceanic meadows. Examinations of the stomach contents of sardines and other small fish reveal the fact that a very large percentage of the food used by these animals consists at times of dinoflagellates. In many parts of the ocean and at some seasons of the year these flagellates far outrank the diatoms in abundance, and become the dominant forms for longer or shorter periods of time. At such times they may become a menace to the slow-moving or bottom-living animals. The unusual amount of oil and

other products secreted by them and released in great quantities through the rapid decay of the organisms, as is often the case in an outbreak of "red water" along the California coast, proves overwhelming to those animals which are not able to escape from the infested area (Kofoid, 1911). These animals, which include such forms as the holothurians, sipunculids, mollusks, the sting ray (*Urolophus halleri*) and guitar fish (*Rhinobatis productis*), die in great numbers and are cast up by the tide upon the beaches.

In the more common occurrences of small patches of red or yellow water which may persist on the surface of the ocean for a few days and then disappear as mysteriously as they came are to be found evidences of the great plasticity of these organisms, and their physiological reactions to slight changes in the chemical content of the oceanic waters. These reactions and interrelations are obscure. and but little can be done besides pointing out a few of the lines along which further evidence must be looked for.

"Red Water."—The occurrence of isolated patches of discolored water at the surface of the ocean is frequently observed during the summer months along the shores of southern California. These areas vary in color from a slight greyish turbidity of the water to a decided yellow, red or dark brown color. The extent of the water thus affected may be limited to a few hundred yards, such as occurred during July, 1914, at La Jolla, and in July and August, 1917, from Long Beach to Santa Barbara, California, or it may extend for a hundred miles or more along the coast, as in the outbreak of red water in the same region in August, 1907 (Kofoid, 1911). These discolored areas are usually found near shore with a seaward extension of one-half to three miles.

The length of time during which these areas may persist ranges from a few days to several weeks. Torrey (1902) records the appearance of red water from July 7 to September 1, 1902, from the region of Santa Barbara to San Diego.

This discoloration has been popularly attributed to submarine earthquakes, landslides, or the presence of sulphur or phosphorus discharged from submarine mineral springs in the water. It is, however, caused by the sudden appearance of vast multitudes of dinoflagellates in the surface plankton, and may be due to the sudden and periodic enrichment under favoring conditions of temperature and light of the coastal waters by the nitrogen-bearing upwellings common along the shores of that part of California.

The presence of such vast quantities of these minute organisms within a limited space results in the death of countless myriads of them, the ensuing decay producing a nauseous and penetrating stench of a most disagreeable nature. These products of decay are toxic to many marine organisms, which die in great abundance and are stranded on the beach by the tide. The filtrating action of the beach sands also results in the accumulation of vast quantities of these organisms along the tide lines and the sands become foul with odors of their decay.

The species of dinoflagellate which has been found most frequently to be the cause of the manifestation of red water is *Gonyaulax polyhedra.* During the summer of 1914 an outbreak of "yellow water" occurred which lasted from July 27 to August 6, caused by a small species of *Gymnodinium*, which is here described as *G. flavum.* This was found to occur in small patches, the greenish yellow color of which was very conspicuous on the crest of the breakers near shore. A sharp line of demarcation separated these patches from the uninfected waters. Okamura (1916) found that areas of colored water in Yokohama harbor, Japan, in June, 1910–1911, were due to the presence of *Cochlodinium catenatum.* These were present in such vast quantities that the effect upon the marine life in the waters was marked, many fish dying as a result.

Somewhat similar to these appearances of colored areas of sea water is the occurrence of *Amphidinium* on the beach sands at Port Erin, Isle of Man, as recorded by Herdman in a series of papers in 1911–1913. These were found in such vast quantities that the sands were colored a greenish brown. They occurred about or a little above the half-tide mark. These deposits were of a varying size, one of the largest covering a continuous stretch of sand about fifty yards long by five yards in breadth. They were visible for periods ranging from a few days to a month, increasing or decreasing or even changing the location according to the stages of the tide. More than one species of *Amphidinium* was found to be present in these colored areas, the predominant one being *A. herdmani* (*A. operculatum*).

Under ordinary circumstances no zone of decay is found in the beach sands, since the adjustments of bacterial, plant, and animal life in this region are such that reciprocal growth and decay preserve the balance of the arenaceous habitat, as they do in the pelagic one, without marked localizations of regions of fermentation and decay. That the diatoms play a part in these interchanges and interrelationships within the arenaceous habitat is well known. The only references, however, to the part that dinoflagellates may take therein are those of Herdman, who followed for several years the recurrences of patches of *Amphidinium* followed by nearly equal numbers of diatoms in the same region. From April 7 to November 2, 1911, *Amphidinium* appeared thus four times. This rhythmical occurrence of two different forms in the same territory is strongly suggestive of the alternations that may sometimes be observed in plants, one plant alternating with another in recurrent occupation of the same region.

NUTRITION.—The subject of nutrition in the dinoflagellates is one fraught with many misconceptions and inaccuracies, due to the imperfect knowledge of the group. West (1916) in his recent book on the *Algae* in the series of Cambridge Botanical Handbooks places the Dinoflagellata with the Algae, stating that over 90 per cent of them are true vegetable organisms with holophytic nutrition.

One cannot work with the marine unarmored Dinoflagellata for even a short time without being struck by the fact that the majority of the individuals observed show evidences of holozoic nutrition, in the Gymnodinioidae at least, and that the number actually containing chromatophores is relatively small throughout the entire Dinoflagellata. Contrary to West's statement, it is probable that a large number of them have not holophytic but saprophytic or holozoic nutrition. It is notable also that a few forms, as *Amphidinium steini*, may possess chromatophores and at the same time show the presence of foreign bodies in the cytoplasm (Stein, 1858–59). This has been true in our own material also (pl. 4, fig. 44; pl. 5, fig. 50), though the actual ingestion of foreign organisms has not been observed.

The cell contents of an alga consist of nucleus, chromatophores, pyrenoids, starch grains or related assimilates, and perhaps a few oil globules. On the other hand, the presence of distinct chromatophores of the typical algal form is a comparatively rare occurrence in the dinoflagellates, even in the thecate forms, where the ingestion of solid particles of any considerable size would appear to be a difficult if not impossible procedure. The evidences for holozoic nutrition lie in the presence of food bodies, often of recognizable organisms, within food vacuoles in the cytoplasm, and the accumulations of the products of metabolism in the form of oil globules, vacuoles, refractive granules, and rodlets in the central or peripheral plasma. These, correlated with the absence of chromatophores, would seem to offer conclusive evidence of holozoic nutrition in the greater number of species of the unarmored type.

The genus *Amphidinium* is probably more nearly holophytic throughout its range than any other genus as a whole. A few apparent exceptions are found here, however, as in *A. steini*, mentioned above. Stein has figured this species with definite organisms in the body as well as chromatophores, though the latter are smaller than those in individuals without ingested food bodies. It may be that this indicates a periodic recurrence or at least facultative occurrence of both types of nutrition. Evidences of a similar condition may be noted in *A. scissum* (pl. 2, fig. 22). *A. cucurbitella* (pl. 1, fig. 6) shows undoubted evidences of holozoic nutrition. Two large masses are present in the cytoplasm, one surrounded by a water vacuole as though recently ingested. In *A. cucurbita* (pl. 1, fig. 9) the body is filled with radial rodlets and large masses, one of which lies in a vacuole, interspersed with refractive granules, the whole presenting an appearance hardly compatible with holophytic nutrition. Other species in this genus which show some slight evidences of holozoic nutrition are *A. crassum* (fig. U, 18), *A. sulcatum* (fig. U, 10), and *A. vasculum* (pl. 4, fig. 36).

In the genus *Gymnodinium* a relatively smaller number of species occurs which possess undoubted chromatophores. Most of these are found in the more generalized group, the subgenus *Gymnodinium strictu sensu*. Here also, as in *Amphidinium*, the two types of nutrition are occasionally found associated in the same species, as in *Gymnodinium fulgens* (fig. X, 30), *G. agile* (pl. 3, fig. 31), and in *G. herbaceum* (pl. 4, fig. 44).

West (1916) concludes that the nutrition of the colored forms is holophytic. One of the most highly colored species found in the Gymnodinoidae is seen in *Gymnodinium lineopunicum* (pl. 6, fig. 65), in which the remains of an ingested *Pouchetia* are found occupying the anterior part of the body. In *G. violescens* (pl. 6, fig. 69) also food bodies are present, though not definitely recognizable as distinct organisms. Other species in this group showing the same indications are *G. contractum* (pl. 5, fig. 52), *G. sulcatum* (pl. 8, fig. 83), and *G. rubricauda* (pl. 8, fig. 88), the first two of which contain bodies still surrounded by a definite vacuole. In *G. incisum* (pl. 3, fig. 27) the remains of a *Pouchetia* with the ocellus still visible clearly indicate the origin of many such bodies in the plasma of these forms as the partly digested remains of ingested organisms. It is thus evident that color alone can not be taken as indicative of the type of nutrition which may be possessed by the organism displaying it. Further evidences of this will be found in the genera *Cochlodinium* and *Pouchetia*.

In the remaining species of *Gymnodinium* comprised in the subgenera, *Pachydinium* and *Lineadinium*, the absence of chromatophores is quite general and indicates saprophytic or holozoic nutrition for most if not all of these species. In *Gymnodinium helveticum* (fig. Y, 11) Penard (1891, pl. 5, fig. 13) has figured an ingested rhizopod, *Difflugia arcula*. For most of the species of the subgenus *Pachydinium* (figs. Z, AA) nutrition seems to be holozoic. In *Gymnodinium lira* (pl. 3, fig. 30) we find an unusual condition in the ingestion of what appears to be a grain of sand, which fills a large part of the body.

Dogiel (1906) found food bodies present in both *G. coeruleum* and *G. heterostriatum* (*G. obtusum*). In the latter species our own material has offered abundant evidence of its preference for solid food. Plate 5, figure 56, shows such an one which had captured a *Cochlodinium* individual. Members of this species were numerous in many hauls throughout the summer at La Jolla, and in only a few cases was the body free from such ingested material. The size of the ingested organism was often huge, and under the stress of conditions in the microscopical field it would frequently be ejected from the body by a vent at the antapex. During this process, which occupied but a moment, the entire posterior end of the body was rent open, presenting a similar appearance to that shown in *Pouchetia maxima* (pl. 6, fig. 61). This vent immediately began to draw together and in a few minutes had completely disappeared, the body resuming its normal outline at the antapex. The ingestion of these huge bodies has not been observed, but it is probable that it takes place by an amoeboid-engulfing action of the sulcal area similar to the process noted in other flagellates, as in *Tetratrichomonas prowazeki* (Kofoid and Swezy, 1915).

In the genus *Gyrodinium* the number of species with chromatophores is very small, both relatively and numerically. The same possibility of the union of both holophytic and holozoic nutrition previously noted is suggested in *G. melo* (pl. 5, fig. 50) with its green chromatophores and large food body. *G. intortum* (fig. CC, 10), whose green color might indicate a vegetable method

of feeding, has ingested a dinoflagellate which still shows its characteristic girdle.

In the species containing an abundance of yellow ochraceous pigment, as in *G. ochraceum* and *G. fulvum*, as well as those with red pigment, as *G. corallinum*, *G. virgatum*, and *G. britannia*, the cytoplasm is usually clear, with few inclusions, and gives no evidences of the formation of starch granules or related products. Food bodies may be occasionally found in *G. corallinum* as well as in *G. ochraceum*, though most of the specimens of these species noted present no clue to their manner of feeding. In *G. virgatum* (pl. 10, fig. 112) the posterior end of the body is distorted, presenting the same appearance found in *Gymnodinium heterostriatum* after the ejection of a food mass.

In another species, *G. maculatum* (pl. 6, fig. 62), also plentifully supplied with pigment of a violet color, food bodies were occasionally found within the cytoplasm, which, at other times, was remarkably clear and free from cell inclusions of all kinds. It is probable, therefore, that these forms have a saprophytic or holozoic mode of food-getting. The numbers of individuals of some of these species that were observed, however, were too small to be conclusive on this point.

We find in the members of the genus *Cochlodinium* evidences of holozoic nutrition similar to those observed in the three preceding genera. One of the most striking instances of this is that seen in *Cochlodinium rosaceum* (pl. 8, fig. 85) with its ingested *Pouchetia*. This is one of many instances in which members of the latter genus have been devoured by other dinoflagellates, and might suggest its desirability as a choice article of food. It is, however, probably no more frequently captured than are the members of the other genera, but the latter quickly lose their characteristic features and become indistinguishable in a food vacuole. With *Pouchetia*, on the contrary, the ocellus retains its characteristic appearance until final disintegration of the body, making it easy to identify the generic, though not the specific, status of the digesting food mass.

In the species *Cochlodinium vinctum* (pl. 2, fig. 15), of which a number of individuals were examined, it was found that a large food body of similar appearance was present in each specimen examined. This was located in the anterodextral part of the body. It is a reniform, greenish or oil yellow, vacuolated body with its surface covered with small, highly refractive spherules resembling oil drops. These are arranged over the surface with considerable regularity. Its center contains an elongated pinkish vacuole and in one instance what appears to be a nucleus of the dinoflagellate type. Other bodies were sometimes present in the cytoplasm.

In *Nematodinium partitum* (pl. 6, fig. 68) a species of *Gymnodinium* is shown, with its girdle still intact. Other members of this genus also present evidences of food masses within the plasma.

In *Pouchetia* we find the most striking instance presented in the group thus far. One specimen of *P. voracis* was found with the theca of a *Peridinium*

partly crushed together within its body (fig. PP, 2). The contents had evidently been digested and the remains were being forced to the posterior region of the body preparatory to ejection when the *Pouchetia* escaped from the cyst. The *Peridinium* here captured is a large species, the length of the body equaling that of the organism which has devoured it, as may be seen from the length of the half-shell which is visible in the figure.

*Pouchetia,* like the genus *Erythropsis,* has no species which possesses chromatophores. A few of the species of the former and all the latter failed to show the presence of food bodies in the cytoplasm. With the small number of species and individuals observed, however, this is not conclusive evidence as to its manner of food-taking. It is probable that nutrition is either saprophytic or more probably holozoic in both genera.

The same conditions that have been observed in the forms discussed herewith obtain in the other members of the Gymnodinioidae. One of the most rapacious feeders is *Noctiluca.* This seems to devour indiscriminately anything of an organic or even an inorganic nature that comes in its way: the authors have observed on two occasions the presence of grains of sand within it nearly as large as the body. Both these individuals were lying on the substrate apparently unable to rise above it.

In this brief review of these forms it has been shown that there is an upward progression from a chromatophore-bearing, holophytic type of nutrition in *Amphidinium,* which has probably been carried over from the holophytic cryptomonads, to a saprophytic and holozoic type in the more advanced members of the group. In some species both types are intermingled, others are more clearly marked off as having a single type of nutrition. The demarcation between the saprophytic and holozoic types is still more difficult to define since those belonging to the latter group resemble the saprophytic forms when food bodies are not present. It is possible that all three types may be found in a single individual.

The presence of pusules in these organisms is significant in this connection. The process of taking the surrounding medium into the body through the pusules, its passage through the cytoplasm and escape at the surface is probably correlated with a saprophytic method of food-taking. The relatively huge size of the pusule apparatus in the thecate forms may be due to the lack of free access of the surrounding fluid to the cytoplasmic body. Many species of the dinoflagellates are never captured in surface hauls, but are found within the deeper layers of water, which are also the layers most rich in decaying plankton and hence most suited to saprophytic organisms.

A fourth mode of food-getting is also present in this group, that is, the parasitic type found in the Blastodiniidae. Some of these, as *Blastodinium pruvoti* (Chatton, 1906), may be only a commensal in the intestine of the host, *Paracalanus parvus,* or they may be truly parasitic, as in *Chytriodinium roseum,* which feeds upon the contents of the egg of a copepod (Dogiel, 1911). Still

others are ectoparasitic, as *Oodinium pouchcti* on Appendicularia (Pouchet, 1885*a*).

The dinoflagellates are thus found to have evolved all the types of nutrition that are known in other groups of living organisms. The manner in which this has taken place is difficult to conjecture, since the fact that all types may be found in the same plankton haul. under precisely similar conditions, precludes an explanation of environmental changes or isolation as the determining factor. Neither are there any evidences which would make sexual selection responsible for the change. The factors which afford a plausible explanation of these phenomena in the Metazoa are difficult to apply to these simply organized creatures without apparent sexual differentiation or behavior.

The possible relation of the process of digestion and the color of the organism is shown in the characteristic color that is found in what appear to be food balls in some species. In many cases these bodies vary in size and often in position in individuals of the same species with relatively little variation in color. These are evidently not secretions, such as starch grains, etc., but appear to be food bodies in process of solution. The characteristic color for the species may possibly be due to the specific chemical reactions of the digestive fluids, and as such may vary but slightly for different members of the same species.

The presence of a definite mouth or cytostome in the Dinoflagellata is obscured by the dislocation of the flagella from the functional anterior end of the body and their migration to a midventral location. It is still more modified and seemingly obliterated in many species by the separation of the two flagella and the resulting presence of two distinct flagellar pores, the anterior one from which the transverse flagellum takes its origin, and the posterior from which the trailing, propelling flagellum emerges. Between these two lies the intercingular part of the sulcus and from each of the pores a slender canal leads to an expanded pusule. These pusules may have their deeper ends approximated or even joined in a continuous cavity from pore to pore.

While no dinoflagellate has been seen by us to capture food with the lips of the intercingular sulcus it appears from its relation to the pores and flagella and its probable derivation from the cytostomal region of more primitive flagellates that this region is the morphological equivalent of the mouth or cystostome and functions as such in the capture of the relatively large organisms found within its food vacuoles. The astonishing plasticity of the oral region observed by us in some parasitic trichomonads, and reported by Rhodes (1920) in *Collodictyon*, encourages us to hazard the inference that the intercingular sulcus is correspondingly mobile and efficient as a food-capturing mechanism in the unarmored dinoflagellates. From the evolutionary standpoint it has been one of the most plastic parts of the organism and it is perhaps equally mobile in the individual.

Reactions to Stimuli.—This is still an untouched field as far as the dinoflagellates are concerned, as it is for the majority of Protozoa in general.

Beyond the application of stimuli for the production of light by the organisms, no laboratory experiments with them have been carried on by us. In their reaction to light a few facts only have been brought forth.

One of the most interesting of these is that recorded by Herdman (1913) for two species of *Amphidinium*. He had noted, during a succession of years, the rhythmic appearance of patches of these organisms on the beach sands at Port Erin, Isle of Man. In addition to this rhythmic occurrence another rhythm was observed in the appearance above, and disappearance below, the surface of the sand; it was these latter movements that were investigated. It was found that this was a direct response to environmental stimuli and could be very fairly calculated from a knowledge of the actinic value of the light and the condition of the tide. The optimum light was a diffused one, with an avoidance of strong illumination. The organisms were also found to disappear before the incoming tide reached them and to reappear as soon as the tide receded from their area. These two interacting stimuli, light and tide, produced a daily and a fortnightly rhythm. If conditions were experimentally altered a new rhythm intervened.

During the summer at La Jolla hauls were made at four-hour intervals through the day and night from the surface of the water at the end of the pier at the Biological Station. These were supplemented by hauls made at varying distances of one to eleven miles offshore, both surface hauls and from a depth of sixty or eighty meters to the surface. The latter were made only during the day, usually about 8 o'clock in the morning, though this was not invariable. These hauls were carefully examined and records made of the occurrence of the dinoflagellates contained therein.

These records during the month of July for the collections at the pier show only a slight variation in the number of species present at the different intervals throughout the day, the smallest number being that for 4 a.m., the highest at 8 a.m., with a slightly smaller percentage at 8 p.m. and 12 p.m. than for the 12 m. and 4 p.m. records. These records are inconclusive owing to the amount of foggy weather prevailing during that month. This was found to influence materially the number of holozoic dinoflagellates (or those without chromatophores) appearing at the surface. Most of the forms possessing chromatophores, and therefore dependent upon sunlight, are found to be neritic or littoral in their habitat, with a predominance of holozoic organisms in the strictly pelagic plankton. As a result of this, surface hauls made during the day contain the neritic forms and relatively few holozoic species.

In the hauls made farther offshore, where neritic influences were not so potent, it was found that the surface hauls usually contained relatively few forms, both as to species and as to individuals, while the deeper hauls made at or very near the same place at approximately the same time were usually well supplied with dinoflagellates.

These conditions indicate a negative heliotropism, with marked avoidance of strong sunlight in many of the species at least.

Luminescence.—One of the most strikingly familiar sights of the sea beach at night during the warm months of the year is the display of phosphorescence in the breakers. Many of the small plankton forms are capable of producing this light, such as crustaceans, worms, and coelenterates, as well as some of the bacteria. No inconsiderable part of it, however, is due to these minute dinoflagellates. It is probable that the bacteria play little if any part in the ordinary exhibitions of phosphorescence of the sea, since the light they produce is a continuous one and not a sudden flash, such as may be observed in the breakers or in the water elsewhere when it has been disturbed.

*Noctiluca* was the first one of the group which received recognition as a light-producing organism, observations having been made on it as far back as 1717 (Dahlgren, 1915–16). Since that time casual notes and detailed studies on this form have been numerous, as a result of its wide distribution, great abundance and relatively large size, combined with the brightness of the light which it produces. It is probable that other forms somewhat similar in structure to *Noctiluca*, as *Leptodiscus* and *Craspedotella*, are also luminescent, but thus far no evidence has been brought forth to bear out this conclusion.

It was not until some time after these first observations made on *Noctiluca* that the light-producing qualities of the remainder of the dinoflagellates were noted. This was due to the work of Michaelis in 1830. He figured at least nine species of *Peridinium, Ceratium,* and *Prorocentrum,* with a description of the light produced by them. These observations were confirmed by later investigators, but without the exactness of detail that has been given for *Noctiluca.*

Among the Peridiniidae and Gymnodiniidae very many, if not most, of the genera contain light-bearing species. Observations on these groups have been almost wholly confined to the thecate forms, due to their greater abundance and the comparative ease with which they may be studied. Those that have received the most attention are *Ceratium tripos*, *Gonyaulax polyhedra*, *Peridinium bahamense*, and a colonial species of *Peridinium* observed by Dahlgren (1915–16) in the waters of the Delaware and Chesapeake bays.

Experiments made by us at the Biological Station at La Jolla, California, have also been mainly on the thecate forms. The method of study has been the isolation of individuals in a watch glass with a small amount of filtered water, which has been examined both before and after the experiment to make certain that no other organisms were present. These isolated individuals were then tested by various stimuli, jarring the watch glass or adding fresh water, alcohol, ether, or other chemicals in very dilute quantities. It was found in this manner that nearly all the species of *Peridinium*, *Ceratium*, and *Gonyaulax*, then common in the plankton hauls, were capable of producing light. Light was never observed in a watch glass containing a single organism without the application of stimuli, though it was abundantly exhibited in the glass dish near by containing the usual plankton haul. This would indicate the necessity

for stimuli of some sort for the production of the light, whether through contact with other organisms or débris, or through agitation of the water.

To determine the periodicity of the production of the light, watch glasses containing a single individual, as well as finger bowls containing a quantity of the plankton, were placed in the dark room and tested at various times during the day. These were sometimes taken into the dark room during the day, or as frequently were placed there on being brought in at the 12 and 4 o'clock night hauls. They were thus kept continuously in the dark for twenty-four hours. The results were invariably the same in both cases, that is, light ceased to be produced with the early dawn and began again with the coming of late dusk in the evening. No amount of stimulation was able to bring forth the slightest response during the day. With the coming of dusk stimulation would produce a few flashes at first, and with the deepening darkness the number of these increased until the bowl would show its maximum illumination. The reverse of this procedure took place with the coming of dawn.

The light given forth by these dinoflagellates is silvery white and lasts no more than a single second. Dahlgren has noted another method of lighting, which he calls the death glow or glow of exhaustion, caused by lifting *Ceratium* out of the water on to the hand or a bit of clean cloth or paper. In these cases the glow lasted from several seconds to several minutes. This probably explains the phenomenon observed in the hauls that were made each night. When the net was drawn up, rubbing it with the finger caused streaks of light which lasted usually for a much greater length of time than the ordinary flash seen in the water. This is probably produced by the organisms caught in the meshes of the net and thus held captive. The amount of light seen in this way is much greater than that produced at any one time in the jars containing the hauls. The long-horned *Ceratium* and other forms would most easily become entangled in the threads of the net, allowing the smaller, smoother forms, such as *Gymnodinium,* to escape altogether.

During an outbreak of yellow water near the Biological Station, July 27 to August 6, 1914, caused by the presence of enormous quantities of *Gymnodinium flavum* (see p. 209), the breakers along the shore were brightly luminous. A few forms of both *Gonyaulax* and *Noctiluca* were found in the hauls, but not in sufficient numbers to account for this display. At the height of the outbreak *Gymnodinium flavum* was present almost to the exclusion of other forms. It seems, therefore, certain that the phosphorescence observed was due to this organism, though, unfortunately, no tests were made in the laboratory to confirm this conclusion.

The very close similarity of structure between the naked and thecate dinoflagellates leads to the belief that the capacities for luminescence in the two groups are much the same, and that the ability to produce light is not confined to a few species alone. In the tests that were made at La Jolla during the summers of 1916 and 1917 it was evident that no single group of dinoflagellates

was present in sufficient quantity to account for the amount of light produced at one time. On the contrary, it must have been the combined result of all the groups, since many genera and species of dinoflagellates were abundant, often to the exclusion of other known, light-producing organisms.

The probable seat of luminosity has yet to be determined. In *Noctiluca* it is found as spots of light on the surface, which may be localized or may include the entire periphery of the organism. The presence of oil globules or allied substances is common throughout the dinoflagellates, especially near the surface, and it is probable that the material from which luciferine is secreted is drawn from these bodies. No observations have yet been made, however, upon the condition of these before and after the exhibition of light.

CHAPTER V

# COMPARATIVE ORGANOLOGY: OCELLI, PUSULES, NEMATOCYSTS

In any group of organisms differentiation within the group comes about through modifications of their characters more often than by the addition of new ones. In the Protozoa, which in the number of individuals far exceeds that of any other phylum, the number of structures upon which these changes may be rung is exceedingly small in comparison with the Metazoa. To permit the production of the vast number of different kinds of protozoan organisms, then, modifications have appeared, manifold in variety, usually minute and often obscure, yet making a grand total that gives to this group a diversity of form and appearance as great as, if not greater, than may be found in any other phylum.

In all this baffling array it is no small task to unravel the tangled lines of growth and variations and place the fundamental structures in their proper relationships. The task is often rendered further impossible by the lack of adequate data and by misinterpretations of both form and function which obscure much of the earlier literature. The work must of necessity, therefore, be only fragmentary, providing a basis upon which future investigation may place the growing structure.

The fundamental features of the Protozoa consist of motor organelles with their related structures, organelles for food-getting, assimilation and excretion, nuclei and skeletal modifications. Some of these structures, as external motor organelles and nuclei, have less significance from the standpoint of comparative morphology, especially of the smaller groups and of species, since their relations and homologies are obvious and fundamental. The other structures of the protozoan body are subject to greater modifications, and their interrelations become increasingly complex as speciation progresses.

This is especially true of those organelles which, present in a simple or modified form in the Protozoa, have been carried on into the Metazoa and find there their highest development. Beyond the definite structures directly correlated with the functions pertaining to the comparatively simple type of organization found in the ordinary cell, structures of this type are not numerous, and have always been the occasion for much skepticism. Among such structures may be mentioned the ocelli and nematocysts of the dinoflagellates, and the nervous and muscular elements found throughout the Protozoa generally, reaching their highest development in the group in the neuromotor apparatus of the higher flagellates and ciliates. It is, however, in these fundamental types of living organisms, with their vast periods of evolutionary development and

asexual—and possibly sexual—generations behind them, that the beginning of many of the metazoan organs must be looked for and not in subsequent aggregates of differentiated cells.

In no place is this obvious relation of the Protozoa and Metazoa more strikingly illustrated than in nuclear conditions which obtain throughout the two groups. The older method of beginning all cytological study of nuclear phenomena with *Ascaris*, or other metazoan types of a relatively late period of evolution, is an inversion of the natural order. Recent investigations are continually bringing to light knowledge of nuclear and mitotic phenomena in the Protozoa, which may ultimately result in a considerable reorganization of many of our present day concepts of these conditions in the Metazoa.

Ocelli.—In the possession of a well developed eyespot or ocellus the Pouchetiidae stand unique among the Protozoa. In its type of structure this organ is distinctly metazoan in character, apart from the fact that it forms only part of a single cell instead of being made up of a number of cells united in specialized tissues. From the larger viewpoint of the body as an integrated organism, and not as groups of cellular tissues, this aspect of its lack of cellular organization is of relatively minor importance.

Schütt, in his monograph on *Die Peridineen* (1895), places the stigma, or eyespot, as it is sometimes termed, of the fresh-water dinoflagellates, as in *Glenodinium cinctum*, in the same category as the ocellus of *Pouchetia*, as did Bütschli (1885) in his earlier discussion of this subject. Later biologists, as Lang (1901), Doflein (1911), and Lühe (1913), add to this category the stigma of fresh-water flagellates, as in *Euglena* and *Eudorina*. The basis of these later comparisons seems to lie in the early investigations of Francé (1893), which have not, however, been confirmed by later investigators working on the same forms.

Francé figured for *Euglena*, *Eudorina*, *Pandorina*, and *Trachelomonas* stigmata of a peculiar type. In each of these flagellates this structure consisted of a mass of red pigment imbedded within which were small spherical bodies. These bodies varied in number from one to two or more in the different species. They were spherical or ellipsoidal in shape and highly refractive. In *Euglena* these bodies were composed of paramylum and in the Phytoflagellata of amylum.

The later work of Wager (1899) and Hamburger (1911) on *Euglena* and of Kofoid (1898, 1899) on *Pleodorina* and *Platydorina* cast considerable doubt on the validity of Francé's work. Both Wager and Hamburger found in *Euglena viridis* that the stigma is composed of small red granules imbedded in a protoplasmic layer. The stigma lies on the border of the cytopharynx in close relation with a slight enlargement of the flagellum. No "crystallin" or "lens bodies" could be found in any of the material under examination. In *Pleodorina* and *Platydorina* the stigmata are simple masses of pigment granules, with no differentiated structure. Other examples might be mentioned, but

these will suffice to show that Francé's work cannot be accepted without further investigation and confirmation on this point.

The stigma of the fresh-water dinoflagellates, as in *Glenodinium cinctum*, *Gymnodinium paradoxum*, and *Gyrodinium hyalinum*, is likewise a simple undifferentiated mass of granular pigment, located in the ventral sulcal area, near the origin of the longitudinal flagellum. These structures seem to be homologous with the stigmata of the flagellates, apparently identical in structure and probably in origin. The widespread occurrence of this organelle throughout the fresh-water Flagellata would suggest a correlation between its development and its environment, since it is rarely if ever present in the marine forms.

On the other hand, the entire absence of a stigma of this type in the simpler dinoflagellates of oceanic waters would suggest the improbability of its forming one of the developmental stages of an organelle which is found only in the highly specialized pelagic species of the Pouchetiidae. No adequate evidence is forthcoming to show the presence of intermediate stages between these two types of structures.

These facts then point towards the conclusion that the ocelli of the dinoflagellates is not a derivative of the stigma commonly present in the fresh-water species of this group, as well as in other flagellates. Evidence seems also to point to a connection between scattered pigment occurring in many of the marine species and the progressive formation of the melanosome of the Pouchetiidae. We have, therefore, confined the term stigma to the simple mass of pigment granules present in the lower forms, and use the term ocellus for the more highly specialized organelles of the Pouchetiidae.

In its structural efficiency, as found in *Erythropsis*, it is probably fully equal to the ocelli found in the medusae of the Hydrozoa, which may consist of a cluster of pigmented cells or a cup of pigmented cells filled with a spherical thickening of the cuticle to form a lens. The difference is here mainly one of size, that of the medusa having several cells uniting to perform a function which in *Erythropsis* is confined to parts of a single cell. The minute structure of the lens and its exact relations to the melanosome have not been investigated in the Pouchetiidae, beyond observations on the living organism. When this has been done it may reveal structural similarities which will indicate more clearly its relationships than can be shown with our present knowledge of this organelle. That it is a light-receiving organ and a fairly efficient one the details of its structure would indicate.

PUSULES.—The cytostomal area of the dinoflagellates is represented in the sulcus and the flagellar pores on the ventral surface, its internal extensions taking the form of pusules. The reasons for these conclusions have been pointed out elsewhere. The fundamental underlying organization is directly comparable with that of similar structures elsewhere in the Protozoa, and consists essentially of a groove in the surface leading to the opening through the plasma. Each group of Protozoa in which this structure is found has its own peculiar

modifications of the fundamental type, such as membranellae and cilia in the ciliates; and the modifications in the Dinoflagellata are no less peculiar and typical.

The modifications characteristic of this group consist of two grooves at the junction of which are located the openings into the pusules. The first of these grooves is the transverse one or girdle, extending in a more or less spiral course around the body (fig. B, *gir.*). Occupying the furrow of the girdle is the relatively wide, ribbon-like flagellum. This is in constant motion with waves passing from its proximal to or towards its distal end. This motion, combined with the spiral course of the girdle, keeps a constant current of water passing over the opening. The second furrow is longitudinal and joins the two ends of the girdle. The flagellum which arises from the posterior pore and occupies the posterior portion of the longitudinal groove or sulcus is threadlike, and hence offers the least possible obstacle to the free movement of the current of water down the sulcus. Both of these grooves are bordered by lips usually wide and well developed. In the thecate forms these are still further marked off by broad lists or fins. The relatively narrow opening or pore into the anterior pusule lies at the anterior junction of the girdle and sulcus at the base of the groove. The posterior pore lies near the distal junction. These pores are thus located at the points which would give optimum conditions for their functioning as cytostomal areas.

The anterior pusule is somewhat more prominent than the posterior one and is probably the one in which the function most closely approximates that of the cytopharynx of other groups or is most highly localized. Its close connection with the anterior flagellum finds its parallel in the juxtaposition of flagella and cytostome in the trichomonad flagellates (Kofoid and Swezy, 1915), and more strikingly in *Chilomonas paramecium*, where the flagella emerge directly from the cytostomal opening with their insertion near its base. The same connection of flagellum and pusular opening is found also in the longitudinal flagellum. The reason for this intimate connection is patently the need of a propelling force to insure a constant current of water down the ventral groove and over the openings. The constant wavelike motion of the transverse flagellum, combined with the shape of the furrows, lends itself admirably to this purpose.

The full homology of the cytostome of the simpler flagellates is, however, to be found in the intercingular sulcus as a whole, and the two pores at the bases of the two widely separated flagella are to be regarded as the anterior and posterior ends respectively of the primitive cytostome shifted from its original anterior location to the midventral region and stretched out longitudinally between the migrating flagella. It is twisted about the body in *Gymnodinium* and *Cochlodinium* and may be extended anteriorly in the anterior limb or loop of the sulcus towards the apex and posteriorly in the posterior limb towards the antapex. It is improbable that these extensions have any share in cytostomal functions of the intercingular sulcus, from which they take their origin.

NEMATOCYSTS.—The nematocysts, like the ocelli of the dinoflagellates, are among the most highly specialized organelles found in the Protozoa. Like them also the nematocysts of *Polykrikos* and *Nematodinium*, similar in structure to the nematocysts of the Coelenterata, represent a type of specialization that is metazoan in its character and occurence rather than protozoan.

The fact that these organelles are of rare occurrence in the Dinoflagellata and are totally unknown in the remainder of the Mastigophora naturally raises the query whether they may not be adventitious bodies, ingested either with fragments of coelenterates as food, or after discharge into the water from some coelenterate of the plankton. This suspicion of extraneous origin is heightened by the fact that such cases are known in the Metazoa, as in the mollusc *Aeolis*, in which the nematocysts are introduced into the body with its food (Grosvenor, 1903).

Several facts point towards the conclusion that the nematocysts of both *Polykrikos* and *Nematodinium* are not adventitious bodies, but are normal structures in the organisms in which they are found. First and foremost of these is the fact that they occur in at least four different species, have been found in every individual of these species thus far examined, and have not been found in other forms feeding on the same plankton and often showing the same kind of ingested organisms.

Fragments of coelenterates have not been observed as food particles nor have free nematocysts been found in the plankton in which *Polykrikos* and *Nematodinium* occur. Contact with the sea water is usually sufficient to bring about a discharge of the coiled filament of the nematocyst. The young stages of the nematocysts deliquesce very rapidly in sea water on disintegration of the body of *Polykrikos*. If they are adventitious it would be necessary for them to resist the disintegration of the sea water prior to ingestion, provided they were found free in the water. If ingested in coelenterate tissue the matured nematocysts must endure ingestion without discharge. The structure of the nematocysts is always constant, which might not be the case if they were adventitious unless they were always derived from the same species of coelenterates. This would postulate a habit of selective feeding of which we have not the slightest evidence. On the contrary, *Polykrikos* is omnivorous in its feeding habits.

Fauré-Fremiet (1914) was the first investigator who attempted to solve the mysteries of the development of these peculiar organelles, as also did Chatton in a series of papers in 1914. The latter figured a cycle of development (fig. G) which leaves many points still open to question. Both of these investigators maintain as the result of their investigations the conclusion that these are normal structures in *Polykrikos*, and not parasitic or adventitious in their origin.

Fauré-Fremiet also pointed out the similarities between the nematocysts of this genus and those found in *Campanella umbellaria* (*Epistylis umbellaria*).

These were described by Bütschli (1887–89) as occurring in pairs scattered through the peripheral protoplasm.

The only other organelles of a similar nature occurring outside the Cnidosporidia are the trichocysts abundant in many species of the Ciliata. These are not characteristic flagellate structures. Both Chatton (1914*c*) and Fauré-Fremiet (1913) describe trichocysts in *Polykrikos,* however. These slender

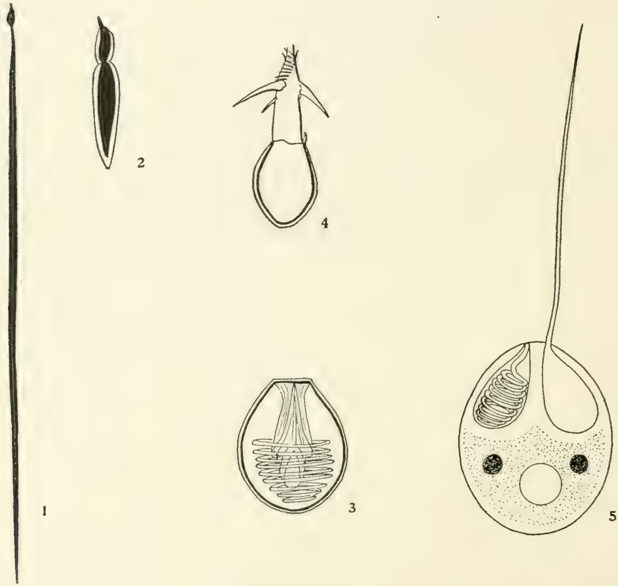


Fig. H. Trichocysts and nematocysts. 1. Exploded trichocyst of *Frontonia leucas* Ehrbg. After Tönniges (1914, pl. 18, fig. 1). × 1250. 2. Unexploded trichocyst of same (pl. 18, fig. 4). × 1300. 3. Nematocyst of *Hydra attenuatus.* After Toppe (1910, pl. 14, fig. 45*c*). × ? 4. Exploded nematocyst of *Hydra grisea.* After Toppe (1910, pl. 14, fig. 46*b*). × ? 5. Nematocysts of *Myxobolus.* After Doflein (1911, fig. 820 A). × ?

refractive bodies or rodlets, as we have termed them, are found throughout the genera *Gymnodinium* and *Gyrodinium* as well as *Polykrikos.* They seem to have no resemblance, either in structure or function, to the trichocysts of the ciliates. No evidence is forthcoming to link them with the developing nematocyst. Their general occurrence in many species of two genera which do not possess nematocysts would preclude the possibility of so classifying them.

A homology between the nematocysts of *Polykrikos* and *Nematodinium* and the trichocysts of the ciliates appears also to be untenable, since the structure of the two organelles differs so greatly. The origin of the latter structures is still obscure, Maupas (1883) and Schewiakoff (1889) claiming an ectoplasmic origin for them, while Brodsky (1909) found their origin in the endoplasm. Their position is consistently in or closely abutting upon the ectoplasmic layer in most if not all ciliates. In *Polykrikos*, as in the genus *Nematodinium*, the position of these organelles is not definitely localized. Neither can any definite statement be made as to whether their origin is ectoplasmic or endoplasmic. In the undischarged trichocysts of *Frontonia leucas* (fig. H, 2) a certain superficial resemblance to the nematocysts of *Polykrikos* is found. This resemblance is entirely lost when the trichocyst is discharged (fig. H, 1). A long filament is thrown out beyond the surface of the body, while the posterior portion of the trichocyst also elongates, the whole structure becoming several times its original length, diminishing in width at the same time.

In the Cnidosporidia the polar capsules, while resembling the nematocysts of the dinoflagellates in general appearance, yet differ from them in their fixed position, and in the fact that they are formed within a capsulogenous cell, from a definite part of the developing sporocyst. In the spores of *Myxobolus* (fig. H, 5) the coiled thread of the nematocyst, lacking the differentiated introvert of those in the dinoflagellates, is everted as a slender, tubular extension of the capsule. This may be thrown completely out of the spore at the time of discharge (Keysselitz, 1908).

In the nematocysts of the Coelenterata the anatomical features show only a slight advance over those found in the dinoflagellates. The introvert may be armed with spines variously arranged on the coiled filament when it is everted (Toppe, 1910). In the resting stage the appearance of the whole structure is not unlike that of the nematocysts of *Polykrikos* (fig. H, 3). The accessory structures with which they are associated in the coelenterates, as the cnidoblast, form one of the chief differences between the two organs. The question of homology between the two structures is one that needs more critical data for its solution. The lack of a definite cnidoblast would not necessarily point to an absence of homology, since that would probably be a secondary acquisition, resulting from the multiplication of cells of the body and their specialization, and unnecessary where one cell carries on all the functions of the body. A certain amount of this specialization has taken place in the Cnidosporidia, where the body of the developing somatella becomes divided into two parts, each with a definite number of nuclei with definite functions in the developing spore. Here also a further advance in the development of the nematocysts has taken place in that they have acquired an enveloping capsulogenous cell.

## CHAPTER VI

# LIFE CYCLES: EFFECTS OF PARASITISM ON LIFE CYCLE, BINARY AND MULTIPLE FISSION, ENCYSTMENT, SEX

The question of polymorphism is one ever present in dealing not only with the Protozoa but with most of the lower invertebrates as well. Protozoology as a science is still so new and its accumulated data, though already vast and daily increasing, so vague in outline and so interwoven with error, consequent on its very newness, that this and related fundamental questions can only be touched upon lightly, with the full knowledge that conclusions reached today must wait upon further investigation for confirmation or refutation. That this must be so does not conflict with the need for summarizing present achievement in any field, nor the formulation of conclusions drawn from existing data. Indeed, these serve only to give a fresh impetus to investigation and to indicate the lines along which important results may be found.

The possible connection between length of period of evolution and the complexity of the life cycle resulting therefrom finds some striking confirmation in the Protozoa as compared with the Metazoa, in which polymorphism tends generally to disappear among the later evolved and more highly specialized groups, except as related to sex. That other factors may enter into a consideration of this problem does not alter the fact that polymorphism occurs in inverse ratio to the length of time of evolution of the group, subject to secondary modifications associated with adaptive processes as a result of parasitic and social life and considerable changes of habitat.

In only a few forms among the Protozoa has a complete life cycle been followed through from its initial zygote to the beginning of the next cycle. This has resulted in the rather general conclusion that the life cycle is simple in all but a few groups, the different stages being summarized in the two processes of growth and binary fission. There is almost no positive evidence that this is true for a single protozoan. On the contrary, it is becoming increasingly evident that a much more complex state of affairs exists.

This question of polymorphism has a very direct bearing on any critical study of the dinoflagellates, since one family of the Gymnodinioidae, the Pyrocystidae, has been formed for what later evidence clearly indicates are not generically distinct organisms. This organism is the large, globular form, *Pyrocystis*, which breaks up into sickle-shaped cysts (fig. I), the contents of which divide again to form small, *Gymnodinium*-like flagellates, usually eight in number. Evidence is accumulating, some of it still unpublished work by the senior author, which shows that such a stage is an integral part of the life cycle of genera as different as *Gymnodinium* and *Gonyaulax*. It is probable

that most, if not all, dinoflagellates pass through a "pyrocystis" stage or its equivalent in their development.

Our knowledge of the development of the so-called *Pyrocystis lunula* (*Gymnodinium lunula*) is still incomplete, but it serves to represent what we already know of the life cycle of this group. In our somewhat diagrammatic figure representing this cycle (fig. I) the beginning of the series is placed where it very obviously does not belong. The beginning probably lies in the still unbridged gap represented by the question mark. There is some evidence, very slight to be sure, and needing further confirmation, that conjugation may occur at this stage between the large globular organisms, and probably not in the small flagellated forms, as might be expected, just escaped from the cyst (fig. I, 8).

This large spherical organism, without visible means of locomotion, first attracted the attention of Murray on the voyage of the Challenger Expedition of 1873–1876. His notes on it were published in his reports of the results of the expedition in 1876 and 1885, with the name *Pyrocystis* suggested as an appropriate designation. It has since that time been found to occur in all oceanic waters where dinoflagellates have been studied, its distribution being coextensive with that group.

Pouchet (1885*a*) described a crescent-shaped cyst as "*Peridinium* voisin de *Gymnodinium spirale*," showing a single large *Gymnodinium* together with other typical *lunula* cysts, one of which he figured with five smaller *Gymnodinium*-like flagellates contained within it. In Schütt's monograph on the *Peridiniales* (1895) he figured as *Gymnodinium lunula* the crescent-shaped cysts, and later (1896) changed their generic designation to *Pyrocystis*, as *P. lunula*, thus recognizing their relation to the forms earlier described by Murray, but as independent organisms, not as two phases of the same cycle. He divided the development of *Pyrocystis* into two stages, the first the tetraspore stage in which the cells are rounded to spindle-shaped, and the second or *Gymnodinium*-like stage developing from the first.

The development of the spindle or crescent-shaped cysts from the large spherical ones was not established until Dogiel (1906) and Apstein (1906) published the results of their studies on the same forms. They followed the development from the pyrocystis stage through the successive mitoses to the formation of the small *Gymnodinium* and its escape from the crescent or secondary cyst. The account of the life cycle presented herewith is largely taken from Dogiel's admirable work, supplemented by the results of our own observations.

The change of the small *Gymnodinium* (fig. I, 11) to the large spherical form has thus far escaped observation. This (fig. I, 1) is a naked form without a cyst wall, though at first glance it might pass for an encysted individual. The periplast is thick and closely adherent to the body. The nucleus is found at one side close to the periphery, in a rather dense, granular mass of cytoplasm. From this mass long streamers of cytoplasm run out, following the periphery

mainly and forming a loose network over the entire cell, the branches anastomosing at various points. The interior of the cell is sometimes filled with a single large vacuole, sometimes by several, with strands of protoplasm extending through it from the main portion around the nucleus.

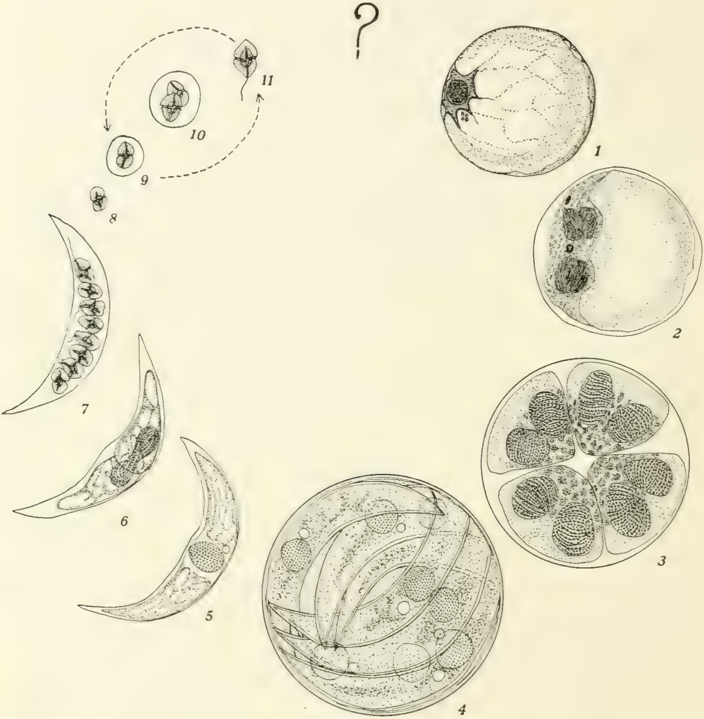


Fig. I

Fig. I. Life cycle of *Gymnodinium lunula* Schütt. After Dogiel (1906, pl. 1) with some modifications. *Pyrocystis* stage, 1–7. *Gymnodinium* stage, 8–11. 1. Large globular form. Resting spore? 2. Formation of first cleavage nuclei. Protoplasmic body shrinking away from cyst wall. Primary cyst stage. 3. Second cleavage with fourth division of nuclei completed. 4. Formation of crescent-shaped spores. Secondary cysts. 5. Single spore released from the cyst. 6. Beginning of division of the spore. 7. Completion of spore divisions with the formation of eight *Gymnodinium* individuals. 8. *G. lunula* escaped from cyst. 9. Formation of tertiary cyst. 10. Division of encysted individual. 11. Individual escaped from cyst. Encystment may take place, repeating 9–11 many times before the next stage is begun. The change from 11 to 1 is unknown. × 330.

With the formation of a cyst wall the body shrinks somewhat in size, leaving a space between itself and the containing cyst (fig. I, 2). Division of the nucleus takes place by a process of mitosis, and is usually repeated twice before the body divides, so that four nuclei are present at the first division of the cytoplasm, which results in the formation of four daughter cells. The nuclei of these daughter cells divides again (fig. I, 3), producing eight nuclei or even sixteen with a fourth division. With the division of the cytoplasm eight or sixteen daughter cells are produced. These elongate and become encysted in slender crescent-shaped, thick-walled cysts which are completely filled by the body when first formed (fig. I, 4).

The mother or primary cyst ruptures soon after the completion of the formation of the daughter or secondary cysts which float out freely into the water. No evidence has been forthcoming to show that these secondary cysts are capable of independent motion when the rupture of the primary cyst wall releases them. On being set free the next stage in their development takes place. The cytoplasm of the encysted cell soon begins to shrink away from the wall (fig. I, 5), concentrating at the center of the body around the nucleus, which divides (fig. I, 6) once, twice or three times (fig. I, 7). The small bodies thus produced develop into the typical *Gymnodinium* with a full complement of furrows and flagella. These escape with the rupture of the cyst wall and form the motile individuals of the cycle. They may become encysted (fig. I, 9) and divide during the encysted state (fig. I, 10) or while free-moving. Simple binary fission may be repeated many times, probably before the next stage is entered upon, which results in the production of the phase shown in figure I.

Division of the contents of the secondary cysts into eight individuals is not an invariable rule, apparently, since cysts are sometimes found containing two, three, four, or six fully formed *Gymnodinium* individuals. This is probably the result of the delay or omission of the second division or the division of one or more secondarily formed nuclei. In some of the larger species (pl. 2, fig. 14) a single individual may be formed within the cyst. The result of the process outlined in figure I is normally the production of 64 or 128 individuals from a single cell. The length of time necessary for the completion of this process has not thus far been determined. Dogiel (1906) has estimated the length of time for the development of the sixteen crescent-shaped cysts (fig. I, 4) from an individual in which the first division has taken place as six hours. This part of the life cycle is probably much longer than the part resulting in the production of the large spherical form from the small *Gymnodinium*, since it is relatively common, while the other stage has thus far eluded observation.

The crescent-shaped cysts have been found in several species of *Gymnodinium* and also in *Gonyaulax*. One of these belongs to the larger species of *Gymnodinium* as figured by Pouchet (1885*a*, pl. 2, fig. 4), with a single large individual within the cyst. The form shown by Schütt (1895, pl. 25, fig. 808, reproduced in our text fig. Q, 1) as *Gymnodinium lunula* is obviously not related

to that species, its size being considerably greater and its form quite unlike the typical *lunula* (fig. Q, 5). His *Gymnodinium fusus* (=*Gyrodinium falcatum*), shown in his figure 81, plate 25, is still another species, probably representing a secondary cyst stage comparable to that of *G. lunula*. Dogiel (1906) has figured one large encysted *Gymnodinium* in his figure 20, plate 1, which is also not *G. lunula*, but quite evidently another distinct species.

These facts and our own observations demonstrate a wide prevalence of these temporarily to more permanently encysted stages in the Gymnodiniidae, and lead to the conclusion that a type of life history similar to that shown for

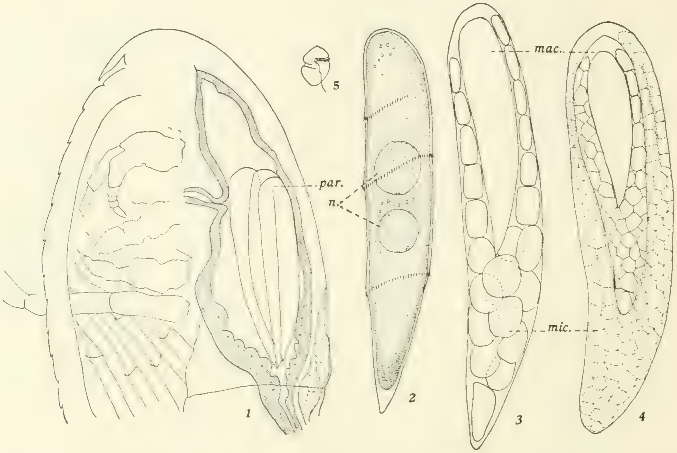


Fig. J. *Blastodinium pruvoti* Chatton. After Chatton (1906, figs. 1–5). 1. *Paracalanus parvus* (Claus), containing three blastodiniums (*par.*) in the intestine. × 200. 2. *Blastodinium pruvoti*, showing circles of spines around the body and two nuclei. × 400. 3. Division of the body into two parts, macrocyte (*mac.*) and microcyte (*mic.*). Division is taking place in the latter. 4. Further development of both macrocyte and microcyte. 5. *Gymnodinium*-like form developed from the microcyte. × 500.

*Gymnodinium lunula* is to be expected for all the members of this group. It is probably a much shorter stage and also much less frequent than that of the vegetative motile phase, and hence is less common. The pyrocystis stage may also be the resting period for the organism, and may require certain conditions or seasons for its production. The whole question is still an open one, however, and requires further investigation for the solution of its many difficulties.

Effects of Parasitism on Life Cycle.—Still further complexity has been introduced into the life cycle with the adoption of a parasitic mode of life by one group of the Gymnodinioidae, the Blastodiniidae. Our knowledge of these

forms is mainly due to the investigations of Chatton, who published his results in a series of papers between 1906 and 1912. Pouchet (1885*a*) had earlier described *Oodinium poucheti* (= *Gymnodinium pulvisculus*) from *Appendicularia*, and Dogiel (1906) added *O. parasiticum* (= *Gymnodinium parasiticum*) from copepod eggs and *Chytriodinium roseum* (= *Gymnodinium roseum*) from copepod or other crustacean eggs.

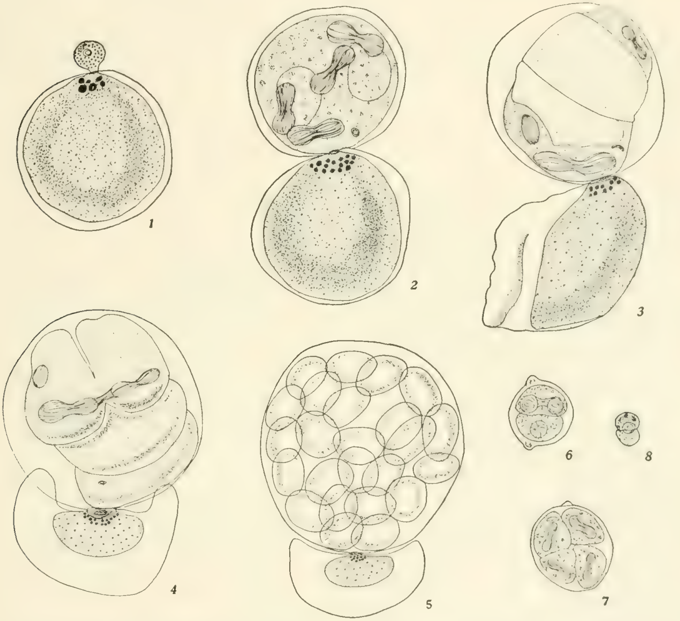


Fig. K. Development of *Chytriodinium roseum* (Dogiel). After Dogiel (1906, pl. 2, figs. 26–35). 1. Small amoeboid individual attached to crustacean egg. 2. Enlargement of parasite with third division of nucleus in process. 3. Division of cytoplasm of parasite, contents of egg greatly diminished. 4. Further division of *C. roseum* with egg greatly shrunken. 5. Completion of first sporoblast divisions. This stage corresponds to that of figures 9, 4, 6. Escaped sporoblast with contents dividing. 7. Further division of sporoblast. 8. *Gymnodinium*-like individual escaped from cyst. × 500.

The complete development of these interesting organisms still awaits more thorough investigation. The contributions to their life history that have already been made indicate a much higher degree of complexity than has been

attained by the free-living forms. The motile individual is a typical *Gymnodinium*-like flagellate of minute size usually and of simple organization (fig. J, 5). When it enters upon its parasitic career it loses its characteristic features. The body becomes greatly enlarged, as in *Blastodinium pruvoti* (figs. J, 2–4) and in this genus divides into macrocyte (*mac.*) and microcyte (*mic.*). These follow individual lines of development that are still somewhat obscure, with the final result, the production of a number of motile *Gymnodinium*-like flagellates (fig. J, 5).

A different type of life cycle is that described by Dogiel (1906) for *Chytriodinium roseum* (= *Gymnodinium roseum*). The parasitic form as originally described consisted of two cells attached to each other, one minute, the other huge (fig. K, 1). Part of the contents from the large cell passed into the small one, which increased in size with a corresponding reduction in the bulk of the other (figs. K, 2, 3). This continued until but a small amount of cytoplasm remained of the larger cell in a somewhat collapsed cell membrane (fig. K, 4). A later and probably more correct interpretation of these two cells (Doflein, 1909; Chatton, 1912) is that the smaller one is the amoeboid dinoflagellate and that the larger one is a copepod egg to which the parasite has become attached. It is thus a case of true parasitism, the dinoflagellate feeding upon the contents of the egg and developing at the expense of its host.

With the increase in size of the parasite the nucleus begins to divide (fig. K, 2), followed by cytoplasmic division (figs. K, 3, 4) of the entire body within a cyst wall which has been formed around it. This process continues until eight, sixteen or more small uninucleated bodies are formed (fig. K, 5). These break out from the primary cyst, form secondary cysts corresponding to the crescent-shaped ones of *Gymnodinium lunula*, and each daughter organism or sporoblast, as Dogiel terms them, begins to divide (fig. K, 6). Division may continue three times, the resulting minute bodies developing into a *Gymnodinium*-like flagellate (fig. K, 8).

In *Oodinium parasiticum* a still further complexity has been introduced in that the parasite enters the eggs and part of its development takes place therein. The entire process is more obscure in this species than in *Chytriodinium roseum*. The products of the final division of the parasite are small flagellates with the typical flagella and girdle of the Dinoflagellata.

The striking similarity between the various stages of the life cycle of *Chytriodinium roseum* and *Gymnodinium lunula* is probably due to the ectoparasitic mode of life of the former. Thus, while deriving its nourishment from the body of the host, it is still exposed to the various influences of the oceanic waters in about the same degree as *Gymnodinium lunula*. An apparently much smaller gap is left in the life cycle of the parasitic form than in that of the free-living one, since the small, amoeboid organism attaching itself to the egg is similar in appearance to the small flagellate which has rounded up and lost its flagella. It is possible, however, that an intervening stage may be present here also.

An endoparasitic mode of life places the heaviest burden upon the developing organism, resulting in greater modifications of the body, usually in larger size and in a more complicated type of development than is generally characteristic of the ectoparasitic or non-parasitic forms. Whether these dinoflagellates are facultative or obligatory parasites is a question, as their further development is entirely unknown.

BINARY AND MULTIPLE FISSION.—Binary fission in the Gymnodinioidae has been noted by many investigators, but critical observation on the details of the process has been lacking. This process has been followed out in the thecate forms by Lauterborn (1895), Borgert (1910), and Jollos (1910), among others. It differs from that found in the typical flagellate in that the plane of division

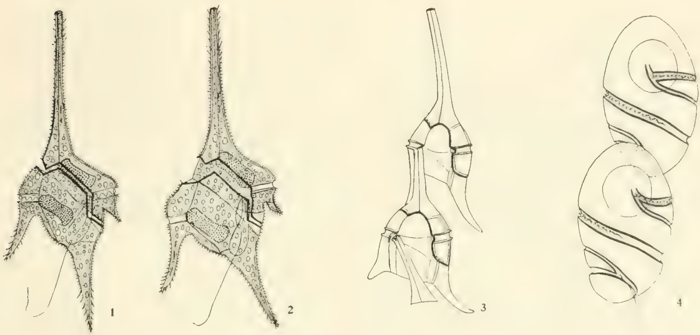


Fig. L. Binary fission in dinoflagellates. 1 and 2. Ventral views of dividing *Ceratium hirundinella* (O. F. M.). After Lauterborn (1895, pl. 13, figs. 13, 14). × ? 1. Division of cytoplasm nearly completed, theca parting along sutures (marked by heavy lines). 2. New thecal plates beginning to form. 3. Ventral view of *Ceratium* in chain. After Kofoid (1909, pl. 1, fig. 1, two anterior schizonts and apical horn of the third). × 405. 4. Daughter schizonts of *Cochlodinium citron* Kofoid and Swezy. After Kofoid and Swezy (1917, fig. 8). × 937.

is oblique and not longitudinal as in the larger group. In the thecate forms this is undoubtedly an adaptation made necessary by the peculiar arrangement of the plates, and enables the two moieties to separate at the sutures (figs. L, 1, 2) and not by the division of single plates, as would otherwise be necessary.

The plane of division of the simpler Gymnodinioidae appears to be more nearly longitudinal, like that of the typical flagellates. In *Prorocentrum* the bivalve theca parts along the longitudinal suture. However, in division in the more specialized Gymnodiniidae, as in *Cochlodinium*, the position of the two daughter cells strikingly resembles that in *Ceratium* (figs. L, 3, 4) at division and leads to the conclusion that division in the unarmored forms is oblique as

it is in the thecate forms. The daughter cells in *Ceratium* are attached to each other at a definite point, the attachment area, which is the distal end of the girdle of the anterior cell and the apex of the posterior cell (Kofoid, 1909*c*). These points form the last bridge of direct protoplasmic continuity before final separation of the daughter individuals. This relation of the two daughter cells is identical in every respect with that which we find in *Cochlodinium* (fig. L, 4). The more plastic body of these naked forms allows greater freedom of movement and mutual adjustment than in the thecate forms. The relative dorsoventral orientation of the two cells is frequently reversed in their struggle for freedom and separation by the rotation of one of the two schizonts and twisting of the protoplasmic strand attaching them to each other.

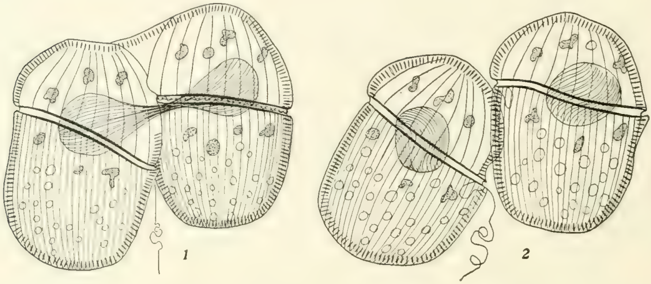


Fig. M. Dividing *Gymnodinium heterostriatum* nom. sp. nov. After Dogiel (1906, pl. 2, figs. 54, 55). 1. Late anaphase of division of the nucleus. Note oblique position of nucleus. 2. Daughter schizonts nearly parted. The final separation takes place at the region of the distal ends of the girdles, as in figures L, 3, 4. × 500.

Further confirmation of oblique fission is found in *Gymnodinium heterostriatum* (fig. M) as portrayed by Dogiel (1906). Here the same relations of structures are found as in *Ceratium*, with the final separation of the two daughter cells occurring at the same place, namely, the anterior end of one and the distal end of the girdle region of the other. As in *Ceratium*, too, the characteristic features of the body become fully developed before final separation of the two daughter individuals takes place.

There is some evidence that division in *Oxyrrhis* is oblique (Keysselitz, 1908) and that the daughter cells occupy a position similar to that of *Cochlodinium citron* at the close of mitosis but prior to plasmotomy.

This condition is strikingly different from that obtaining in other groups of the flagellates, where the separation begins at the anterior end and proceeds to the opposite pole. This process in other flagellates never results in chain formation of the daughter cells, such as is the rule in the dinoflagellates (fig. L).

Some observations on collections made in the early morning lead to the conclusion that fission takes place more frequently during the hours of night or very early morning than at other periods of the day, indicating some relation between nutrition and alternating darkness and light on the one hand and this vital process on the other. Binary fission also seems to occur more frequently during the life cycle than does the more complex process of multiple fission. The former may occur in the unarmored forms in the motile state or after encystment, the latter appearing to be the more common condition when fission occurs.

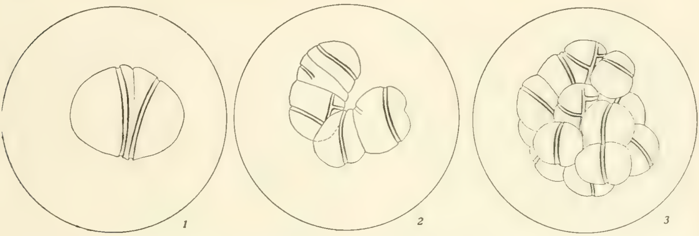


Fig. N. Multiple fission in small *Gyrodinium.* 1. First division with girdles forming. 2. Second division with beginning of third in upper zooid. 3. Sixteen individuals with fully completed girdles, but still closely attached to each other. × 400.

Multiple fission has already been described as part of the life cycle of *Gymnodinium lunula* (fig. I), and consists of successive mitoses of the body, resulting in the production of three to sixteen individuals within the same cyst. Another type of multiple fission has occasionally been found in our material which may represent another phase of the life cycle, or may be a specific modification of the process already described. This consists in the production of few to many small individuals from one body within the ordinary oval, thin-walled cyst (fig. N). Cysts of this type have been noted, which contained dividing individuals of *Gymnodinium*, *Gyrodinium*, and *Cochlodinium.* These apparently differ from the secondary cysts of *Gymnodinium lunula* in that they are more delicate, resembling in every respect the ordinary cyst enclosing a single individual of any of these species (as in fig. Q). The secondary cysts of *G. lunula,* on the other hand, are tough and highly resistant, withstanding for some time the action of preservatives of all kinds. It seems not improbable, therefore, that a process of multiple fission may take place during the same part of the life history as that in which binary fission occurs.

Another type of multiple fission was noted in a single individual only. This was an elongated encysted form, apparently belonging to the genus *Cochlodinium*, with the girdle still intact when first noted, though the sulcus had become obliterated (fig. O, 1). The nucleus of this individual presented a late

telophase stage of division when first found. In a short time the girdle disappeared and the cytoplasm divided into two parts (fig. O, 2). In the course of the next two hours a second (fig. 3) and a third (fig. 4) division took place, resulting in the production of eight moieties, each with a single nucleus. Probably owing to adverse conditions under the microscope, the whole cyst began to disintegrate at this stage, without further development. This would appear to be a type of chain-formation not unlike that in falcate cysts of "*Pyrocystis*," or of thecate forms such as *Ceratium* (Kofoid, 1909*c*) and *Gonyaulax* (Kofoid,

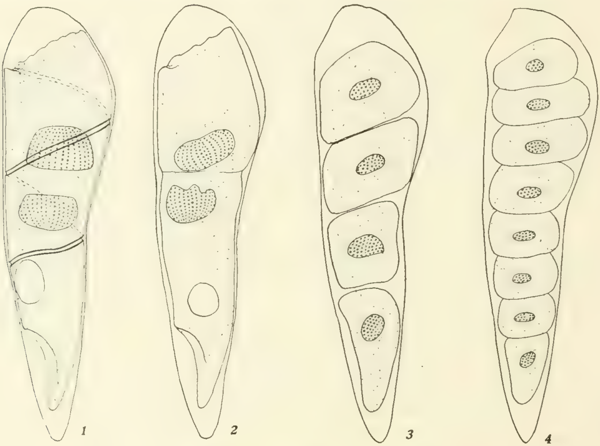


Fig. O. Multiple fission in *Cochlodinium* (?) *elongatum* sp. nov. 1. First division of nucleus. 2. First division of cytoplasm. 3. Second division completed. 4. Third division. Further development of these was not followed. × 500.

1912). It differs strikingly from that in *Polykrikos*, in which the duplication of external organelles usually precedes nuclear division, whereas here this division was unaccompanied by reduplication of cytoplasmic organelles.

Encystment.—It is evident that encystment plays an important part in the life history of these minute organisms. Many forms, especially in the genus *Pouchetia*, are usually found thus enclosed in the plankton, though generally breaking out of their prison when placed under the stimulation of the high degree of illumination necessary for the microscope. When first freed from the cyst the flagellate becomes very active, its movements having a much greater rapidity than has been observed in other individuals that have not recently passed through this period of rest.

Encystment in the dinoflagellates, at least in the marine forms, is probably due to one of two causes. The first of these is the need for protection during the non-motile stage of the period of multiple and binary fission. Binary fission may occasionally take place in non-encysted forms, but is by far more frequently seen in encysted ones. Multiple fission has never been observed in the non-encysted state in our material nor is it illustrated in the literature.

The second cause of encystment is correlated with a holozoic type of nutrition. It is apparently induced by the ingestion of large food bodies, and indicates a need for a quiescent period for its assimilation. There are several reasons for this conclusion. One of these is the prevalence of food bodies within encysted individuals. These may give indications of having been recently ingested with few signs of digestive changes having taken place (pl. 8, fig. 85), or they may represent partly digested bodies in what are evidently older, larger cysts (pl. 8, fig. 87), or the final remains towards the end of the period of digestion (pl. 8, fig. 89). When these encysted forms are observed under the microscope a difference may usually be detected in their activities. A recently encysted individual with a large food mass within its body is seldom active and has never been observed to break out of the cyst. On the other hand, those individuals which give indications of having neared the end of the period of digestion within the cyst are active, rotating within the cyst and often, while under observation, escaping from it altogether.

Another fact pointing towards the correlation of encystment with holozoic nutrition is the relative infrequency of encystment in members of the group having chromatophores, such as *Amphidinium* and the lower species of *Gymnodinium,* and its frequency among the higher genera of the group, such as *Cochlodinium* and *Pouchetia.* Other causes leading to cyst formation are probably operative on all groups alike, hence the greater frequency of its formation among holozoic types would lead to the conclusion that a correlation exists between these two factors named.

The cyst is first formed as a thin membrane secreted by the body wall and closely investing it (fig. W, 1). The flagella are apparently lost at the beginning of the process and the membrane is closely adherent to the outlines of both girdle and sulcus. The flagella are probably absorbed, though no observations on this point can be presented except the occurrence of individuals with short stout flagella. Very soon after the formation of the membrane the cyst begins to enlarge as a result of the incoming fluids which fill the spaces between the cyst wall and the body. With this distension the cyst gradually loses the outlines of the body and becomes nearly symmetrical, either ellipsoidal or spheroidal, varying in different species, but fairly constant in shape within the species. The body also may lose its own characteristic outlines and furrows and become rounded up (fig. P). The retention of the bodily features is the condition more commonly found.

In some cases the cyst may reach relatively enormous proportions, and secondary (pl. 8, fig. 89), or even tertiary (pl. 5, fig. 54; text fig. Q, 7) cysts may be formed within the first one.

Some time before the organism breaks out of the cyst new flagella make their appearance. These at first are very short (pl. 8, fig. 85), but reach their normal length before the rupture of the cyst wall (pl. 8, fig. 87; pl. 9, fig. 101). With the development of its motor organelles the minute organism usually becomes active, rotating in the cyst with nearly constant movement of the flagella. In one instance *Cochlodinium pirum* (pl. 9, fig. 101) was held under observation for several minutes before it escaped from the cyst, the size of which allowed great freedom of motion. Its behavior was quite similar to the activities of a small animal suddenly placed in a cage for the first time. It swam round and

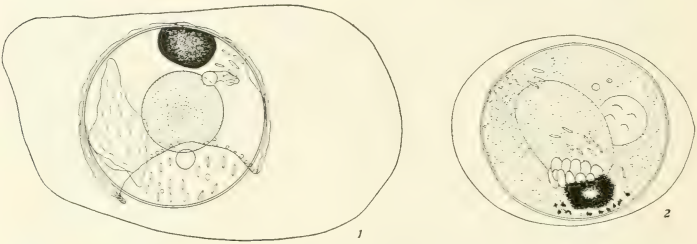

Fig. P. 1. Encysted *Pouchetia rubescens* sp. nov. × 700. Food body present. Secondary cyst formed. This became ruptured and gradually shrank away to one side of the enclosed organism. 2. Encysted *Nematodinium partitum* sp. nov. × 710.

round the cyst with the apex almost touching the wall but apparently without exerting any pressure upon it, though the final result was the same as would have occurred had actual pressure been exerted, that is, the wall suddenly burst and the flagellate escaped from its prison.

Irregularities in the shape and size of the cyst may sometimes occur, though not so frequently as might be expected in these delicate organisms. The unusual cyst enclosing *Gyrodinium caudatum* (pl. 9, fig. 102) may be due to some abnormality, but more likely it corresponds to the secondary cyst shown in text figures I, 5, 6, 7, in which a single individual only has been developed (cf. pl. 2, fig. 14).

As may be seen from figure Q, three kinds of cysts are formed. The large globular cyst (fig. Q, 2) and the crescent-shaped ones are more resistant than the others. The former is probably the resting stage of the organism. These are frequent in preserved material and sometimes abundant.

The second type of cyst, which is also highly resistant, is the crescent-shaped one. The wall of this is usually double-contoured and much thicker than the

other types (figs. Q, 4, 5). The shape of it varies considerably, and may possibly be influenced by the relative size of the enclosed dinoflagellate or even be the homologue of a *Pyrocystis* stage. Thus in figure Q, 1, the outline is not modified by the contained organism, while in figure Q, 6, considerable change in shape results from the development of the relatively huge *Gyrodinium* within it.

In the third type we find the digestive cyst, or the one commonly enclosing the typical unarmored dinoflagellate when first observed under the microscope (fig. Q, 5). This is thin-walled, hyaline, and varies in size from the closely investing sheath that is first formed to one several times the length of the enclosed organism. This cyst is always very delicate and easily ruptured, in marked contrast to the other, stronger types. Successive cysts of this type may be formed, one within the other (fig. Q, 7).

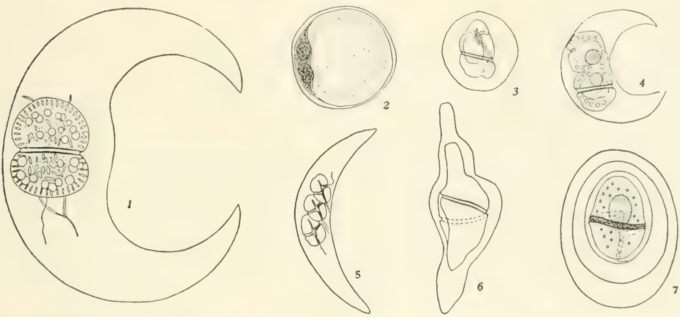


Fig. Q. Types of cysts in the Gymnodinioidae. 1. *Gymnodinium* sp. After Schütt (1895, pl. 25, fig. $80_6$) 2. *Gymnodinium lunula* Schütt. After Dogiel (1906, pl. 1, fig. 2). 3. *Cochlodinium pirum* (Schütt). 4. *Gymnodinium* sp. 5. *Gymnodinium lunula* Schütt. 6. *Gyrodinium falcatum* (Schütt). After Schütt (1895, pl. 25, fig. $81_3$). 7. *Gyrodinium ovum* sp. nov. Formation of three successive cysts. × 250.

Sex.—The question of sex and sexual phenomena in the dinoflagellates is one about which, thus far, but little is definitely known. In only one member of the Gymnodinioidae, *Noctiluca scintillans*, has conjugation been described (Ishikawa, 1891). This process is stated to take place by the cytoplasmic fusion of two isogamic, motile individuals, apparently of the normal type, whose nuclei become apposed but remain distinct. Both the nuclei and the cytoplasm then divide and the syngamic fusion takes place between the two nuclei in each of the daughter cells thus produced. This is undoubtedly an incorrect interpretation of the normal mitosis in which the large paradesmose so indents the nucleus as to give the false appearance of two separated but apposed nuclei.

Spore formation in *Noctiluca* is brought about by a rapid multiplication of nuclei without corresponding cytoplasmic divisions. These nuclei retain their position on one side of the spherical body. With the completion of the division of the nuclei small buds of cytoplasm are formed projecting from one side of the parent cytoplasm, each of which contains a single nucleus. These form the flagellated "spores" which are possibly gametes, which remain attached to the parent cell for some time before their liberation.

In the life cycle of *Gymnodinium lunula* an analogous stage to the spore production of *Noctiluca* may be found in the *Pyrocystis* stage, when the body divides into many crescent-shaped individuals, each of which passes through a further process of division (fig. I) producing small *Gymnodinium*-like flagellates which seem to be equivalent to the swarm spores of *Noctiluca*, and may, like them, be gametes. Whether this rapid multiplication is preceded by conjugation is undetermined.

In other groups of Protozoa where the life cycle has been followed out with some degree of thoroughness it has been found that conjugation is usually followed by rapid multiplication of the nuclei, resulting in the production of numerous individuals. In *Coccidium schubergi* (Schaudinn, 1900) this process is not unlike that followed in *Gymnodinium lunula* as far as the production of the crescent-shaped spores. In the well-known life cycle of the malarial parasite, *Plasmodium vivax* (Schaudinn, 1902), the same conditions are found. Conjugation in *Paramecium*, among the ciliates, is followed by a comparable phenomenon, though here the number of individuals produced is relatively few (Doflein, 1911).

While no indisputable evidence can be offered on the subject of conjugation in the dinoflagellates, yet these comparisons are suggestive. It is highly probable that a process similar to that outlined for *Noctiluca* may also take place in the *Pyrocystis* stage of other dinoflagellates.

A few instances may be found in the literature of so-called conjugation in both the thecate and non-thecate dinoflagellates, but these have too much doubt attached to them to be accepted without further verification. The first of these was figured by Stein (1883, pl. 17, figs. 25–28) for *Amphidinium lacustre*. These figures are identical with what have since been found to be division stages in these forms, the two moieties still remaining attached to each other near the region of the ends of the girdle (figs. L, M).

Among the thecate dinoflagellates Joseph (1878) has reported conjugation for *Peridinium stygium*, and Zederbauer (1904) for *Ceratium hirundinella*. In the latter case Zederbauer has figured a process similar to that found among the conjugate algae. A conjugation tube is thrown out from the ventral sulcal region of each of two individuals. These tubes meet and fuse into a zygospore, the protoplasmic contents of each cell flowing into it. These zygospores become free and have the appearance of the usual thick-walled, encysted forms of the dinoflagellates. Nothing comparable with this phenomenon has as yet been discovered in the unarmored Dinoflagellata.

CHAPTER VII

# EVOLUTIONARY DEVELOPMENT: RELATIONSHIPS, DERIVATION, DEVELOPMENT WITHIN THE GROUP, STRUCTURAL EVOLUTION, NUTRITION AND EVOLUTION, RELATIONS TO THE METAZOA

The phylogeny of the Protozoa is a subject obscured by conditions inherent in the organisms themselves, namely, the unstable and evanescent character of their substance which, with many of the groups, requires but one minute or less to disappear absolutely without leaving the faintest trace behind. This is especially true of the Flagellata. While many of the flagellates have acquired more resistant structures, such as the theca of the dinoflagellates, yet these represent the terminations of the lines of evolution, and their preservation throws no light on the earlier stages of their development or their interrelations. The Flagellata also probably represent the most primitive class, with the possible exception of the lower bacteria, of which we have any adequate knowledge today, and stand at the base of the phylogenetic trees of both the plant and animal world. Thus the length of time during which they have been undergoing evolutionary development far surpasses that of any other group of living organisms of the present day, and at the same time provides for a wider range of differentiation and the more complete elimination of many connecting links. This has resulted in the production of a group of organisms exhibiting, within the compass of a single, minute cell, a wider range of differentiation and of structural features than may be met with in any phylum or even groups of phyla above the Protista.

Another factor tending to obscure our view of the evolution of these organisms, but one which is daily giving way before the constant advance of new discoveries in this field, is the lack of knowledge of the full life history of the Protozoa. The older conception of a simplicity of life history for these forms is gradually being replaced by a more adequate conception of what may be the results on these plastic organisms of a long period of evolution in a changing environment. In line with this comes a change also in the older idea that these are the most simple forms of life. Indeed, the complexity which we now find resident in a single cell, often containing neuromotor organelles or an ocellus in addition to the usual complement of organelles for the purposes of ingestion and digestion of food, secretion, excretion, and other life processes, postulates a relatively higher stage of evolution than that reached by some of the Metazoa. On the other hand, many of the flagellates especially are among the simplest of known organisms both morphologically and in their life history, as far at least as these are known, excluding of course the bacteria.

It is with this background, at once obscure, yet replete with the beginnings of far-reaching lines of influence, that we must search for the early affinities of the dinoflagellates. In lieu of a complete knowledge of the life histories of these forms, which is an important desideratum in any scheme of classification, the morphological features characteristic of the group must be used in tracing out their relationships. Throughout the Protozoa generally the motor organelles have been found to be the most satisfactory basic feature, correlated with other cytological characters, for systems of classification, and it is in the arrangement, number and insertion of these that relationships may be most surely found.

In the dinoflagellates these relations of flagella and places of insertion with the modifications connected therewith are typical and unique. The two main divisions of the subclass Dinoflagellata are based upon the extent of the development of these peculiar modifications connected with the motor organelles. In the Adiniferidea the girdle and sulcus are entirely lacking or merely suggested by the projecting fins and flagellar notch. In the Diniferidea they are usually well developed at some stage of the life cycle. In both groups the flagella have the typical dinoflagellate structure, consisting of a transverse, ribbon-like flagellum and a longer, threadlike, longitudinal, trailing one. At least it is possible so to orient the Adiniferidea as to harmonize them with this interpretation.

Relationships.—The relationships of the Adiniferidea, represented by the genera *Prorocentrum*, *Exuviaella*, and *Cenchridium*, have long been a problem concerning which protozoologists have held widely divergent views. The reason for this lack of agreement appears to be the fact that the Adiniferidea, though they are relatively simple in structure, yet have a bivalve theca. The thecate forms (Prorocentridae and Peridiniidae) are probably derivatives of the athecate ones (Protodiniferidae and Gymnodinioidae), the primitive forms of the latter being more like the other and simpler types of Flagellata.

This possession by the Adiniferidea of an exoskeleton or theca of an entirely different type from that of the Diniferidea, which skeleton indicates an advance in evolution on the one hand, while on the other a relatively simple type of structure and absence of the girdle, has led protistologists in opposite directions in estimating the relationships of the Adiniferidea. Those who have felt the importance of the skeleton in the dinoflagellates as a whole have regarded the Adiniferidea as primitive representatives and have placed them at the base of the phylogenetic tree, as did Bergh (1881*b*) and Bütschli (1885*a*), who first attempted the systematic organization of the group.

When this primitive rôle is assigned to the Adiniferidea a new difficulty arises with regard to the relationships of the Gymnodinioidae, which are devoid of skeleton and contain some of the simplest types of dinoflagellates, as well as some of the most diversified and complex, possessing, for example, eyespots with lens and pigment body, and even nematocysts. Both Bergh (1881*b*) and

Bütschli (1885*a*) solved this difficulty by putting *Gymnodinium* and allied genera at the top instead of the base of their phylogenetic tree, thus giving rise to the conception that the athecate condition is secondarily derived and not a primitive one.

With the increase in our knowledge of the structure, abundance and speciation of these naked dinoflagellates there has come a reversal of opinion in respect to their being derivative instead of primitive types. This is shown in the system proposed by Schütt (1896) in his treatment of the Dinoflagellata (Peridiniales) in Engler and Prantl's *Pflanzenfamilien*. He placed the Gymnodiniaceae as the first or most primitive family, the Prorocentraceae next and the Peridiniaceae as the terminal family. This linear arrangement brings the Prorocentraceae between the Gymnodiniaceae and the Peridiniaceae and thus parts near allies with an entirely divergent family intervening. Klebs (1912) held to a similar view, placing the Gymnodiniaceae in the primitive position and deriving the Prorocentraceae from them by way of *Amphidinium*. Poche (1913) grasps the other horn of the dilemma and places the Prorocentrinea in the primitive position with the Peridiniinea next, within which he brings the two related tribes, Gymnodinioidae and Peridinioidae in the sequence of their evident relations. This arrangement places the thecate Prorocentrinea, however, as the most primitive group. Doflein (1911) gives the primitive position to the same group in his Adinida with the Dinifera containing Gymnodinidae, Peridinidae and Dinophysidae. Cavers (1913), and later West (1916), have suggested still another solution to these difficulties by giving to the Dinoflagellata a diphyletic origin, with the Prorocentraceae having a separate origin from the Gymnodiniaceae.

The dilemma which has thus arisen is plainly one resulting from the fact that we are here dealing with the divergent and largely terminal branches of an evolving group, of the more primitive forms of which we have had too little knowledge to elaborate any satisfactory systematic arrangement which adequately represents the true relationships of these main divisions of the Dinoflagellata.

The search for more primitive representatives of the Dinoflagellata which will show connections with other divisions of the Flagellata and, at the same time, afford a common starting point for the Prorocentridae and the Peridinioidae is well illustrated in the contributions of Klebs (1912), Cavers (1913), and West (1916). Their search leads them among the Chrysomonadina and Cryptomonadina, which include among others biflagellate, asymmetrical flagellates with yellow chromatophores. Klebs adds a new genus, *Haplodinium*, with characteristic dinoflagellate nucleus, two characteristically differentiated flagella, and a continuous, cellulose-like membrane covering the body without subdivisions or pores. He includes this in the Prorocentraceae and modifies the definition of the family to provide for the inclusion of this new, brackish-water genus.

Cavers (1913) gives an extensive review of the interrelations of the flagellates and lower Algae with a predominant utilization of the fresh-water forms, which are perhaps better known than marine ones. In his phylogenetic grouping he derives the branches leading to the Gymnodiniaceae and the Prorocentraceae from two different groups of the cryptomonads, *Protochrysis* and *Wysotzkia*, with a questioned derivation of the diatoms from the Prorocentraceae.

No connecting link between these two groups of dinoflagellates has heretofore been found which would present a reasonable basis for claiming a closer relationship between them. This gap we feel has been bridged by the genus *Protodinifer*, described in this paper, taken together with the genus *Haplodinium*, recently described by Klebs (1912). The former lacks the theca of *Prorocentrum*, but has a similar orientation, with its tentacle extending from the anterior end as the spine does on the theca of *Prorocentrum*.

Thus *Protodinifer* has the appearance of a *Prorocentrum* which has escaped from its theca. A more profound difference separates them, however, in that the former shows the beginnings of a girdle which is poorly developed and apparently a temporary depression only, 0.5 transdiameter or less in length, with a feebly developed sulcus. *Haplodinium* also lacks a theca of discrete plates and tentacle as well as the girdle and sulcus of *Protodinifer*, but its orientation and arrangement of flagella are similar to those of *Prorocentrum* (fig. R, 7).

With these two genera as a starting point two possible lines of development are open. The first of these starts near *Protodinifer* and leads to the Gymnodinioidae by way of *Oxyrrhis* (figs. R, 2–4). The latter genus still shows a poorly developed but posteriorly located girdle. The second line of development goes from *Protodinifer* or other non-thecate forms to *Haplodinium* (fig. R, 5), with its membranaceous, cellulose-like covering of the body, and to the thecate forms *Exuviaella* (fig. R, 6) and *Prorocentrum* (fig. R, 7). Of these genera the athecate *Protodinifer* is obviously to be regarded as the more primitive.

The development of the thecate from the athecate forms is a natural process of evolution which is repeated for each individual in the growth of a new theca or part of a theca at every recurring division.

In thus establishing the relationships of the Adiniferidea and the Dinoferidea a monophyletic origin for the Dinoflagellata becomes a logical conclusion. This, as has been suggested by Bergh (1881*b*) and more fully by Cavers (1913), would probably be found in the cryptomonads, though not as the latter has postulated, as two distinct series of independent origin. Of the two genera which Cavers has suggested as the starting point for his two series leading up to the two separate groups, *Protochrysis* to the Gymnodiniaceae and *Wysotzkia* to the Prorocentraceae, *Wysotzkia* (fig. R, 1) seems more nearly related to the Adiniferidea than probably any other genera of the cryptomonads. With a form nearly allied to these as a starting point the progressive evolution of the

group as a whole may be traced out with the widest gaps near the beginning of the series (figs. R, S).

The fact that both *Wysotzkia* and *Protochrysis* are fresh-water forms renders it highly improbable that these particular genera are to be considered immediately in the direct line of evolution. They can be only persistent morphological types, significant in structure of the common ancestral marine types from which both they and the marine genera have been derived.

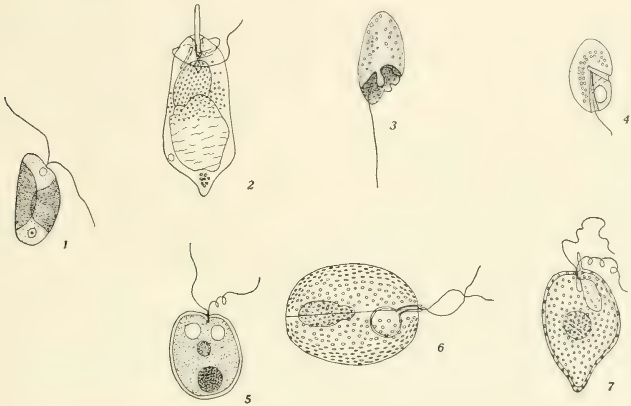


Fig. R. Derivation of the dinoflagellates. 1. *Wysotzkia biciliata* (Wys.) Lemm. After Cavers (1913, fig. $7_5$). 2. *Protodinifer tentaculatum* sp. nov. 3. *Oxyrrhis marina* Dujardin. After Senn (1911, pl. 30, fig. 9). 4. *Hemidinium nasutum* Stein. After Stein (1883, pl. 2, fig. 25). 5. *Haplodinium antjoliense* Klebs. After Klebs (1912, fig. 1 A). 6. *Exuviaella marina* Cienkowski. After Schütt (1895, pl. 1, fig. $1_2$). 7. *Prorocentrum micans* Ehrbg.

So far as present knowledge goes the Dinoflagellata of today probably represent the terminal twigs of the phylogenetic branching (fig. S) of some such simple flagellate, and the genera cited are not intermediate stages leading on to more highly developed forms.

The attempt to find ciliate affinities for the genus *Polykrikos* grew out of a misinterpretation of the structural relations of that remarkable organism. Bütschli (1885*a*) and later Bergh (1881*b*), noting the presence of more than one nucleus, with slight variations in size among them, correlated them with the nuclei of the Ciliata as macronuclei and micronuclei. Cavers (1913) further states that "whether *Polykrikos* forms a link between the Peridiniales and the ciliate Infusoria is, of course, an open question in the absence of further transitional types." Our own work on this genus confirms that published earlier by

Kofoid (1907), namely, that *Polykrikos* is a simple colonial gymnodinium-like organism with the zooids remaining united in a permanent somatella after binary fission, and the number of nuclei equal to the number of zooids, or to half that number. Temporary colonial organization of the linear or chain type is often found in the dinoflagellates and permanent colonies and less or more permanent somatellas are common in other groups of the Protozoa, which have no suggestions of ciliate affinities attached to them. Variation in size of the nuclei, resulting from successive mitoses, is also a common phenomenon and is no more striking in *Polykrikos* than in other protozoan forms.

Cavers further suggests the possibility of the genus *Erythropsis* affording a transition stage between *Polykrikos* and the *Ciliata*. A comparison of the structures of these two widely different organisms (figs. F, RR) will at once demonstrate the futility and morphological folly of looking for the origin of the Ciliata near these highly specialized flagellates, the structure of which differs profoundly from that of present day ciliates. The types of specializations found in the Dinoflagellata, represented on one line by the thecate forms, on another by *Erythropsis*, and on still another by the extremes of torsion in *Cochlodinium*, are not intermediate types which lead on to other groups of Protozoa, but are rather the culmination of their particular lines of development.

Derivation.—The derivation of the Dinoflagellata from some primitive flagellate allied rather closely to existing Cryptomonadina, with two anterior flagella and xanthophyll chromatophores, seems the most probable of all possible lines of origin. The discussions of Pascher (1911), Klebs (1912), and West (1916) serve to establish this, although their utilization of fresh-water genera such as *Wysotzkia* and *Protochrysis* as primitive connecting links seems less tenable. When the marine cryptomonads are better known it may be that as good or better morphological links will be discovered between cryptomonads and dinoflagellates.

The differentiation of one anterior flagellum to form the spirally wound, ribbon-like collar of the craspedomonads, to form the trailing flagellum in the Bodonidae, and to develop into the attached, posteriorly directed, undulating membrane of *Trichomonas*, is suggestive of a widespread and deep-seated tendency for the two or several flagella of primitive types to become differentiated. This differentiation of the two flagella into a trailing thread on the one hand and a closely sinuous ribbon on the other is the basis of dinoflagellate evolution, and establishes the fundamental connections between the Adiniferidea and the Diniferidea. It is to be expected that the primitive cryptomonad with dinoflagellate affinities will show this differentiation in structure or position, or both, of these flagella. These conditions are fulfilled to some extent by *Haplodinium* and *Protochrysis*, the first allied to the Adiniferidea and the second to the Diniferidea, but both are fresh-water forms. We may therefore regard these genera as at least allied closely to the stock of cryptomonads from which the primitive dinoflagellates took their origin, but it is to be hoped that still closer allies will be found among marine flagellates.

It is obvious that the Adiniferidea and the Diniferidea must have been quite distinct, except in the matter of the two types of flagella, even at a very early stage in the evolution of the dinoflagellates, and that the porulate, bivalved skeleon of *Prorocentrum* and its allies evolved independently from that of the thecate forms of the Diniferidea with epitheca and hypotheca. In the Adiniferidea the original functional polarity of the cryptomonad is preserved, while in *Protochrysis, Oxyrrhis*, and the Diniferidea generally, the flagellar pore is no longer terminal but midventral. It therefore seems necessary to regard the Adiniferidea as a basal offshoot from the primitive dinoflagellate arising from cryptomonad stock, which offshoot has paralleled the Diniferidea in the acquirement of a porulate theca. It is quite possible that the plane of division between the two plates or *Prorocentrum*, between the two sides of the theca of the Dinophysidae, and the oblique zigzag suture parting the two moieties of the theca at mitosis in some of the Peridinidae, are all homologous planes, although the actual evolution of the theca appears to have followed the separation of the groups and to have been an independent acquisition in each. The varying modes of separation of the theca into two parts are differentiations of a fundamental, bipartite tendency which we see expressed in the two valves of *Phacotus lenticularis*, in the two chromatophores of many chrysomonads, and in the two parts of the theca of the dinoflagellates and of the diatoms. The obliquity of the plane of fission in the Dinoflagellata may well be a consequence of the ventral position of the blepharoplast and flagellar pores.

Assuming this early separation of the Adiniferidea and Diniferidea prior to the acquisition of the theca in either, we may present our conception of the evolution and relationships of the dinoflagellates in the following diagram (fig. S).

Among existing Cryptomonadina the genus *Wysotzkia* is near the type from which by differentiation of the two flagella such a genus as *Haplodinium* might readily be derived, while *Protochrysis* with its midventral flagella is a natural link to *Oxyrrhis* with the initial stages of the girdle, the fundamental characteristic of the Diniferidea.

The newly discovered genus *Protodinifer* with the anteriorly located flagella, which are differentiated into one posteriorly trailing and the other encircling the anterior end, is a connecting link bridging the gap between the Adiniferidea and the Diniferidea. The flagella are still in or near the primitive position as in the Adiniferidea, but in their differentiation in direction and functon they are of the type in the Diniferidea, although the transverse flagellum has not the broad, ribbon-like form of that group and does not lie in a completed permanent girdle. Since *Protodinifer* has an active functional tentacle-like projection arising near the flagella it cannot be regarded as a generalized or primitive form in this particular, although in all others it may be so designated. It is strongly indicative of the common origin of the two main subdivisions of the Dinoflagellata and might be placed in either with almost equal propriety. However, in view of the location of the flagellar pore near the anterior end of the

body, and the absence of a completed permanent girdle, we have placed it as the primitive non-thecate representative of the Diniferidea and regard the Adiniferidea as an offshoot of this primitive stock.

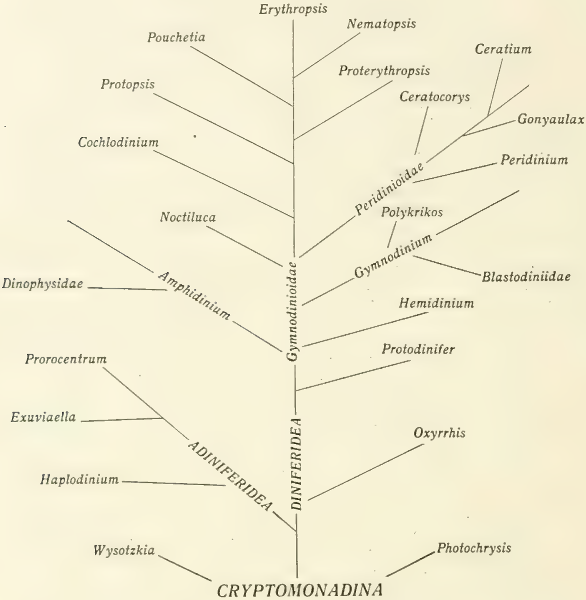


Fig. S. Diagram of phylogenetic derivation and relationships of the Dinoflagellata.

The plastic or generalized nature of *Protodinifer* is indicated also by the ease with which it progresses in either direction, though predominantly with flagellar end leading, and yet again by the fact that the transverse flagellum may be thrown about the body loosely and in either direction, though predominantly in the normal position of the Diniferidea.

With *Protodinifer* and *Oxyrrhis* recognized as primitive members of the Dinoflagellata and of the Diniferidea, it is a natural conclusion to regard the Gymnodinioidae as the basal group of the Diniferidea from which its thecate representatives have sprung, while the process of evolution has continued unabated within its non-thecate forms with resulting high specialization in *Pouchetia*, *Cochlodinium*, and *Erythropsis;* with colonial organization appearing in *Polykrikos;* with simplification in structure in the dinoflagellate phase,

but with complication in life history resulting from the parasitic habit, in the Blastodiniidae.

We have withdrawn *Noctiluca* from the Cystoflagellidae and placed it as one of the Gymnodinioidae, diverging at a low level in the specialization of the group. The "Pyrocystaceae" of Murray, Apstein, and West disappear wholly as merely a phase of the life history of other, and in some cases as yet unknown, dinoflagellates.

Development within the Group.—Within the dinoflagellate group as a whole several distinct lines of morphological development with resulting speciation may be traced. One of these lines follows the differentiation of the structures correlated with the motor organelles. These structures, the girdle and sulcus, form the most characteristic features of the dinoflagellates and are the ones having the greatest value for diagnostic purposes.

The first beginnings of the girdle and sulcus in the genus *Protodinifer* and their continued development in *Oxyrrhis* (figs. B, 2, 3) have already been noted. It is, however, within the family Gymnodiniidae that they reach their typical form and also their greatest development in the Dinoflagellata, together with the torsion of the body which is closely dependent thereon. In this group the line of increasing specialization presents an orthogenetic series notable for its well defined, progressive differentiation that links the members of the family closely together. *Hemidinium*, while probably not the most primitive genus in the family, yet stands near the base of development of these two critical features of the Dinoflagellata. In this genus the girdle is short, its length being 0.5 turn around the body, with the sulcus extending from the girdle to the antapex (fig. C, 1), and with both flagella arising near or at the same midventral point. The development of these structures in *Hemidinium* marks a distinct advance beyond that attained by the genus *Oxyrrhis* (fig. B, 3) in that the girdle and sulcus have definitely marked borders, sharply delimiting them.

In the genus *Amphidinium* (fig. C, 2, 3) the girdle has lengthened to a complete turn around the body, its position being anterior, instead of median, as in *Hemidinium*, thus increasing the length of the sulcus and hypocone and decreasing that of the epicone. In many of the species of this genus, like *Hemidinium*, *Oxyrrhis*, and earlier forms, the flagella arise near together at the proximal end of the girdle (fig. B). In a few species of *Amphidinium*, however, the flagella have become more or less widely separated (figs. U, 1, 4, 6). In the further development of these forms this becomes the usual condition, as in *Gyrodinium* (figs. CC, DD) and *Cochlodinium* (figs. GG, HH). The sulcus also may increase in length, extending from the apex to the antapex.

In *Gymnodinium* we find a type of girdle similar to that of *Amphidinium*, but in this genus its location has become submedian, or at least has moved considerably posterior to its position in *Amphidinium*, with a resulting increase in the relative size of the epicone (figs. C, 4, 5). *G. doma* (fig. C, 4) represents a stage of this posterior migration which is only slightly removed from the condition found in *Amphidinium scissum* (fig. C, 3). In *Gymnodinium* the

girdle may form a closed circle (figs. X, 1, 2, 8, 17) or its distal end may become displaced posteriorly to any distance less than 0.2 of the total length of the body (fig. Y). The extreme of this condition is found in *G. rubrum* (fig. C, 5), which closely approaches the next genus, *Cochlodinium* (fig. C, 6), in its type of girdle arrangement.

The advance from the genus *Gymnodinium* to *Gyrodinium* is but slight in the species at the adjacent extremes of both genera (figs. C, 5, 6). Within the latter genus, however, the progress made in increasing development of the girdle and sulcus is considerable. Here the ends of the girdle are displaced about 0.2 of the total length of the body at the lower end of the scale (fig. C, 6). From this point upward an increasing progressive displacement of the ends of the girdle is found (fig. CC) which reaches its greatest extent in *G. cornutum* (fig. C, 7), where it is slightly more than 0.5 of the total length of the body. The girdle also increases in length so that more than one complete turn of the body is made (fig. C, 7). This results in a torsion of the body and also of the sulcus which is carried about with it. In this genus the torsion never becomes as great as 1.5 turns of the body (fig. CC).

In the torsion of the body the next genus, *Cochlodinium*, exhibits the maximum of specialization found in the Gymnodinioidae. The amount of torsion varies from 1.5 in those species near the border line separating this genus from *Gyrodinium* (fig. C, 8) to four complete turns of the body in the most highly differentiated species (fig. C, 10). Between these two extremes all gradations in the amount of torsion may be found (figs. GG, HH). Torsion of the sulcus also reaches its maximum in this genus, always having approximately one less turn than that of the girdle because of their morphological relations.

The lines of separation of *Amphidinium*, *Gymnodinium*, *Gyrodinium*, and *Cochlodinium* must of necessity be somewhat arbitrary, since the great increase in the number of species results in an increase also in the number of intermediate forms linking together the extremes of each genus. The gap between *Hemidinium* and the other members of the family is much harder to bridge. It is a genus of little known, fresh-water forms of which two species only have been described.

The remaining genus of the family, *Polykrikos*, is a colonial *Gymnodinium* which has secondarily developed nematocysts, and may be considered an offshoot of that genus. Temporary colonial chain formation is frequently seen in *Gymnodinium* and *Cochlodinium* as well as in the thecate forms, *Ceratium*, *Peridinium*, and *Gonyaulax*. The colonial organization of *Polykrikos*, however, seems to have acquired permanency. It shares with the genus *Nematodinium* the distinction of being the only genera in the Dinoflagellata possessing nematocysts.

The five genera of the family Pouchetiidae present another clear instance of progressive orthogenetic differentiation culminating in the most complex types of the Gymnodinioidae, even of the Dinoflagellata, with respect to the

locomotion and sense organs, and with respect to the ocellus, of the Protozoa as a whole. *Protopsis* is clearly a generalized, primitive genus, with girdle and sulcus still at the level of *Gymnodinium* and *Gyrodinium*, the ocellus scarcely integrated and the coloration not advanced beyond the ochraceous stage prevalent in simpler Gymnodinioidae. It is thus evident that this genus is most closely related to the generalized species of *Gymnodinium* and *Gyrodinium*, showing no advance beyond these forms, save in the development of its ocellus. The presence of pigment in the more generalized species of *Gyrodinium* probably is related to the development of the pigmented portion of the ocellus or melanosome in *Pouchetia, Protopsis,* and *Erythropsis*.

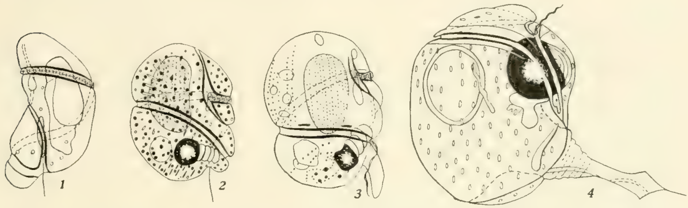


Fig. T. Development of prod of *Erythropsis*. 1. *Cochlodinium cavatum* sp. nov. 2. *Pouchetia maculata* sp. nov. 3. *Proterythropsis crassicaudata* sp. nov. 4. *Erythropsis extrudens* sp. nov. × 500.

In the genus *Nematodinium* (fig. NN) we have an offshoot of a group of divergent species representing a considerable degree of specialization of the girdle and sulcus. These are separated from the remainder of the family by the presence of nematocysts. The only other genus of dinoflagellates with these unique organs is the genus *Polykrikos*. No apparent close relation exists between the two groups, however. This would suggest an independent origin for these structures in *Nematodinium,* unless, as may probably be the case, the connecting links between the two genera have disappeared.

In the genus *Pouchetia* (figs. OO, PP) we find the extreme development of the sulcus in length, torsion, extent of apical and antapical loops, and its constriction of the body. Here the girdle is usually shorter and less conspicuous than the sulcus, unlike its condition in the lower genera where the sulcus is still primitive, whereas the girdle may become more highly complicated as in *Cochlodinium*.

The close relationship of the family Gymnodiniidae and the family Pouchetiidae is clearly indicated in certain points in their structure. One line of specialization linking together these two groups is found in the increasing differentiation of the ventrosulcal region, culminating in the production of the prod of *Erythropsis*. The beginnings of this line may be looked for in the genus *Cochlodinium*. Here an increasing degree of mobility of the plastic sulcal area near the posterior end of the body is present in *C. convolutum* (fig.

HH, 5), *C. helix* (fig. HH, 8), and reaches its greatest development in the genus in *C. cavatum* (fig. T, 1). In *Pouchetia* this same mobility occurs, as seen in *P. maculata* (fig. T, 2). A further development is found in *Protcrythropsis crassicaudata* (fig. T, 3). This line of specialization reaches its climax in the genus *Erythropsis* (fig. T, 4), with its highly developed prod, provided with protractile and retractile fibrillae on the prod, which has developed from the mobile region of the sulcus.

Another form of specialization is found in the development of a tentacle. In the genus *Protodinifer* this is anteriorly located (fig. R, 2). In *Pavillardia* (fig. JJ) it is posteriorly placed, is more mobile, and may reach a greater length than in *Protodinifer.* In *Noctiluca* the greatly modified form of the body, which here becomes a huge sphere, makes it difficult to give to the tentacle an exact location that will link it with that in the other genera. It is closely connected with the remains of a furrow and with the flagellum, hence it probably has its origin in a part corresponding to the sulcal area of other dinoflagellates. There is little evidence if any that these three types of tentacles have any derivative connection other than origin in common territory.

Another line of development that closely links the two groups may be found in the melanosome of the highly specialized ocellus of *Pouchetia* and *Erythropsis.* In the Gymnodiniidae, where the lens formation has not yet taken place, the pigment is scattered through the body, often massing at the apices or near the girdle. The pigment occurring in the family Pouchetiidae has become massed around the lens in the typical melanosome near the girdle. There is no ocellus elsewhere in the Dinoflagellata, or indeed in the Protozoa as a whole, comparable with this integrated organ composed of a laminated, oriented lens embedded in a melanosome enclosing a highly pigmented, presumably sensory core. The stigma of fresh-water dinoflagellates is a single mass, ellipsoidal, or broadly horseshoe-shaped, lying in or near the sulcus, but not consistently at its left. It does not appear to be similar in structure to or homologous with the ocellus of the Pouchetiidae, but the two are rather independent specializations of pigment-producing plasma.

The production of pigments is widespread among the more highly differentiated species of the related genera *Cochlodinium*, *Gyrodinium*, and even in the more generalized species of *Gymnodinium.* Melanin, however, is produced in these lower genera only in two species, *Cochlodinium atromaculatum* (pl. 7, fig. 71) and *Gyrodinium spumantia* (pl. 7, fig. 72). The occurrence of such pigments and of refractive spherules within the cytoplasm of these lower genera has doubtless been the starting point from which the evolution of the ocellate species of this family has proceeded. Various stages of the integration of the ocellus are found within the group.

The evolution of the ocellus within the Pouchetiidae presents several orthogenetic series proceeding along different lines independently of one another but parallel in the different genera, in each case starting with the diffuse, scattered,

scarcely organized, variously directed, posteriorly located, and functionally inefficient form, as found in *Protopsis* (fig. LL), and culminating in the concentrated or more highly integrated, anteriorly directed, and functionally efficient form of the organ. This is best seen in *Pouchetia* and *Erythropsis*, where the known species are sufficiently numerous to afford a range of types.

In most of the species of *Pouchetia* the ocellus presents a high degree of integration (figs. OO, PP). It is in the genus *Erythropsis*, however, that this peculiar organelle reaches its highest type of development as well as its greatest size, as in *E. cornuta* and *E. pavillardi* (figs. SS, 1, 3). Evidence of a lesser degree of integration is also found in this genus, as in *E. labrum* (fig. SS, 6).

Structural Evolution.—The influence of the peculiar types of flagella characteristic of the dinoflagellates and their peculiar position has undoubtedly played an important part in producing the other structural modifications of that group. From this standpoint the most fundamental feature is the ribbon-like transverse flagellum. In the lower forms, such as *Protodinifer*, *Haplodinium*, and *Prorocentrum* (figs. R, 5, 7), both flagella arise at the extremity of the body, and no profound structural modifications thereof result. With the migration of the flagella from this point, however, changes begin to take place. These consist of the formation of a groove or girdle (fig. B, *gir.*) around the body for the lodgment of the transverse flagellum, and another furrow which we call the sulcus (fig. B, *sulc.*) in a longitudinal direction on the ventral surface which contains the longitudinal flagellum. The sulcus also extends anteriorly and sometimes posteriorly beyond the area of its actual functional relations to the flagellum.

The beginning of this process may be seen in *Protodinifer* with its poorly developed, evanescent girdle (fig. R, 2). In *Oxyrrhis* it has extended completely around the body, but is still poorly developed, with ill-defined posterior border (fig. R, 3). It reaches its highest development in the next group, the Gymnodiniidae.

The formation of both furrows is due to the direct influence of the activity of the flagella on the surface of the body. In *Protodinifer* the transverse flagellum has a greater length than the circumference of the body and lies indifferently in several positions. Its activity would be felt on all parts of the circle, but more strongly near its origin, where we find accordingly the beginnings of the girdle. The greater part of the flagellum in this species is not held close to the body, as is the case in the higher members of the group. In the Gymnodiniidae the flagella are frequently short, not more than 0.5 circumference in length, especially in moribund individuals. Many other species, however, especially in *Cochlodinium* (fig. HH, 3) and *Pouchetia* (figs. OO, 5; PP, 3), have the transverse flagellum equal in length to the girdle, and this is probably the normal condition.

The action of a broad, ribbon-like flagellum in constant motion with short, transverse waves, passing through its entire length and held close to the body, would have a profound influence in hollowing out for itself in the plastic body

wall a furrow slightly wider than the amplitude of its vibrations. A similar origin for the longitudinal furrow or sulcus seems evident. In the simpler forms both flagella arise from or near the same point (figs. X, 2, 14), hence we find the sulcus extending from the girdle to the posterior end of the body, with a gradual widening posteriorly to accommodate the movements of the flagellum. With the deepening of this furrow a secondary modification is introduced, in that the depression extends anteriorly above the girdle. In *Gymnodinium bifurcatum* (fig. AA, 3), where the sulcus bifurcates the hypocone, the flagellum is found to swing freely through the cleft thus made, often projecting from the body from the dorsal side, instead of from the usual ventral position.

With the continued increase in the length of the transverse flagellum the length of the girdle has kept pace with it. This, combined with the rotation of the body, has resulted in a spiral course for the girdle with its distal end displaced posteriorly, and gradually pushed farther and farther around the body. The culmination of this lengthening is seen in *Cochlodinium*, where, in its most specialized species, the girdle may make no less than four turns around the body.

The continued lengthening of the sulcus in these highly specialized forms was not necessary to accommodate the longitudinal flagellum, which has retained a position near or slightly posterior to the distal end of the girdle. The consequence is that this flagellum is not involved in the resulting torsion of the body in the intercingular region. In the meantime, with the development of holozoic nutrition, the intercingular part of the sulcus had become the area for the ingestion of food, and hence was necessary in the economy of the organism. Its development, therefore, kept pace with that of related structures. In the Peridinioidae elaborate fins, or lists, further outline both girdle and sulcus, and guide the currents of water which course through them.

In the arenaciphilous group of dinoflagellates certain features are possessed in common by most of the species, which probably owe their development to the influence of their habitat. These forms range in length from 17$\mu$ to 56$\mu$, a size which is considerably below the general average for the Gymnodinioidae as a whole. This small size is evidently an adaptation to the habitat in which the organisms live, enabling them to move more readily through the interstices between the grains of sand and to escape, to some extent, its crushing effects during its not inconsiderable movements. Another adaptation for the same purpose is the strong dorsoventral flattening of the body, giving to it a thin disk shape that is very rarely met with in the characteristically pelagic or neritic forms. Species showing these modifications are found in three arenaciphilous genera, as in *Amphidinium steini* and *A. scissum* (figs. C, 2, 3), *Gymnodinium agile* (fig. Y, 9), and *Gyrodinium viridescens* (fig. DD, 11). The deep sulcal groove with its overhanging flaps is utilized as a holdfast, an adaptation to the conditions of life in shifting sand.

Another significant fact is that most of the species found in this habitat are green in color. This is perhaps correlated with the fact that the beach at

La Jolla, as elsewhere, is fully exposed to the light and that the illumination in this latitude (33°) is fairly direct during midsummer.

In the pelagic and neritic forms a wider range of variation in form is found, combined with a generally larger size and more brilliant coloration. The fresh- and brackish-water species are closely akin to the sand beach forms in their general characteristics. They usually possess green or yellow ochre chromatophores, and are small in size, with a strong tendency towards a dorsoventral flattening of the body. These tendencies are shown in *Amphidinium lacustre* (fig. U, 15), *Gymnodinium tenuissimum* (fig. AA, 7), and *Gyrodinium hyalinum* (fig. CC, 15).

Nutrition and Evolution.—West (1916) has suggested that saprophytic dinoflagellates are probably mostly degenerate forms. There is no evidence for this, however. On the contrary, it seems quite probable that a saprophytic mode of nutrition is a natural one for many of the Flagellata, and, furthermore, that it is the intermediate stage between the holophytic and holozoic types. There are several reasons which point to this conclusion. One of these is found in the intimate correlation existing between the method of food-getting and the structure of the body.

There is in many, if not most, of the holophytic flagellates a close correlation between the presence of chromatophores and a thickened cuticle, or periplast, surrounding the body. This is shown most strikingly in *Euglena*. With the disappearance of chromatophores the periplast becomes thinner, often scarcely detectable as such, and remains so until a definite oral region has become evolved with accessory structures for the ingestion of food. When this stage in the evolution of the protozoan has been reached a corresponding amount of ectoplasmic differentiation takes place, most noticeable in the ciliates with their more complicated structures. A secondary modification is found in the Rhizopoda in the development of pseudopodia, correlated with a thin periplast for the ingestion of food. Very many of the small flagellates which live in stagnant water rich in decaying plankton show an absence both of chromatophores and distinct food bodies in the cytoplasm, as well as an absence of a definitely marked cuticle. So far as evidence goes in these forms nutrition is evidently of the saprophytic type.

In the typical vegetable organism the raw materials enter the protoplast in a state of solution and are there elaborated into assimilable form by means of special organelles and enzymes. This is a more primitive type of feeding than the holozoic method, by which solid food substances are ingested. The transition between the two methods must have been a stage in which the already elaborated material entered the protoplast by osmosis in a state of solution and was ready for assimilation by the cell without the aid of special organelles or enzymes. A thin periplast covering the body is a very necessary factor in feeding by osmosis, and we find this cell covering in its most ideal state among these flagellates. A further advance in evolution is required before the organism

is ready to take in another living body and break down an organization similar, and chemically equal, to its own to render it available for its own use.

The transition stage between these two groups must be looked for in the relatively large group of flagellates not far removed from the base of the phylogenetic tree. The increasing evidence points to the fact that both types of nutrition, as well as the intermediate saprophytic type, are found in forms otherwise closely related, and even in the same individual either at the same time or under the stimulus of different environmental conditions (Zumstein, 1899).

This advance in feeding habits from a saprophytic to a typical holozoic method is found in parasitic as well as free-living Protozoa, and shows a corresponding close correlation with increasing morphological differentiation. Thus in the simpler type of flagellates, as in *Trypanosoma* and *Prowazekia*, lacking a definite oral region, and living in the lymph of the blood and the intestinal canal respectively, nutrition is of the saprophytic type. In some of the trichomonads, as in *Tetratrichomonas prowazekia* (Kofoid and Swezy, 1915), a definite cytostome is present and food masses are ingested, showing an advance to a holozoic mode of nutrition. This type of nutrition is accompanied by a considerable morphological differentiation.

The Protozoa also offer evidences that point to the conclusion that parasitism in this group is not always symbolic of morphological degeneracy, but rather lies often in the upward path of the lines of structural evolution, the reverse of conditions found in some of the Metazoa. In the Blastodiniidae we find this illustrated by the tendency to form a somatella.

In this group the life cycle, as shown in *Blastodinium pruvoti* (fig. J) and *Chytriodinium roseum* (fig. K), becomes increasingly more complex, and the organism attains a larger size, than is the case in free-living forms (fig. I). This condition is found to hold in many instances throughout the Protozoa generally. Among the ciliates the most highly specialized forms are those belonging to the Orphryoscolecidae and living in the stomach of ruminants, such as *Diplodinium* (Sharp, 1914).

Another group which presents increasing evidences of complexity in the life cycle and in anatomical features, which may even be carried to the extent of forming a somatella of several differentiated cells, as in *Myxobolus* (Doflein, 1911), is the Sporozoa. These are wholly parasitic, no free-living species being known.

These two types of nutrition, namely, saprophytic and parasitic, thus seem to be stages in the natural development of the Protozoa, each marking an advance along some line. When these are secondarily acquired in higher forms, however, as in many cases in the Metazoa, such as the parasitic crustacean *Sacculina*, the reverse of this is true and this mode of life becomes symbolic of degeneracy.

RELATIONSHIPS TO THE METAZOA.—The unarmored Dinoflagellata present two structural differentiations which occur also as distinctive characteristics of the Coelenterata, namely, nematocysts and tentacles. The nematocysts of the dinoflagellates are so strikingly similar to those of the coelenterates as to suggest the close relationship of the two groups of organisms. The tentacle of the dinoflagellates arises on the border of the sulcus or mouth of these Protozoa as these organs do around the mouth of the coelenterate.

There is also in the dinoflagellates a tendency to form a multicellular somatella, exemplified in chain-formation in *Ceratium*, in the corresponding more temporary phase in *Noctiluca*, and in the more permanent and more massive somatellas of the Blastodiniidae. We find in *Polykrikos* (originally described as a larval flatworm) a permanent 2- or 4-celled somatella with nematocysts. The sulci of its adjacent cells or zooids form a continuous mouth capable of capturing and engulfing other Protozoa, diatoms, and even the ova of *Sagitta*.

The elemental structures and functions thus presented are suggestive, and possibly highly significant of the path along which pelagic dinoflagellates may have given rise to simple pelagic coelenterates in which cell boundaries and cell layers may have played only a secondary and belated part as the size of the organism increased. If we could put together in one organism the nematocysts, the continuous sulci (mouth), and multicellular (multinucleat) somatella of *Polykrikos* along with the tentacle of *Noctiluca*, one for each constituent cell along the side of the mouth, we should have an organism whose structure would appear prophetic of the Coelenterata and one whose affinities to that phylum and to the Dinoflagellata would be patent.

## CHAPTER VIII

# DISTRIBUTION, LOCAL DISTRIBUTION, HISTORICAL DISCUSSION

The dinoflagellates are widely distributed in both fresh and marine waters, from the polar seas to the tropics, reaching their maximum development, numerically as well as in speciation and in structure, in the warm temperate and tropical regions. No formulation of the laws which undoubtedly govern their distribution can be attempted at the present time, owing to the utter lack of anything like adequate records of the occurrence of this group, that is, adequate from a systematic, distributional or seasonal standpoint. Any conclusions that may be drawn are therefore wholly provisional.

The thecate dinoflagellates have been more fully investigated than have the naked forms, but the records here also are incomplete. It is probable that the two groups are very closely bound together in the temperature and other relations which condition their geographical distribution, but further investigation will be required for the Gymnodinioidae at least before these relations can be stated with any degree of certainty.

Many of the earlier records of the occurrence of these forms, in both fresh and marine waters, are of doubtful value, owing to the often contradictory and poorly defined species characters which usually result in some confusion and error when records of occurrences of species in a large quantity of plankton are made. In the case of doubtful species, where these records are unaccompanied by figures of the organisms found, the records are sometimes practically useless.

In plankton forms which have no fixed spatial relations to the substrate the division into littoral, neritic and pelagic life zones is much harder to maintain than is the case with those organisms whose connection with the substrate is even temporary or whose swimming habits afford some resistance to a passive drifting with the current. Neither of these factors operates to maintain an established position for the majority of the protozoan plankton, hence we find the Protozoa more widely distributed through these three zones of oceanic life than are many other groups. This is true of the dinoflagellates to a very large extent, yet we find even here a slight tendency towards segregation of more or less distinct faunal groups.

The Dinoflagellata are typical pelagic organisms, with some cosmopolitan species and many others of seemingly more limited distribution. They have representatives which are restricted solely to the high seas or are, at most, found only as stragglers in coastal waters, as, for example, *Ceratocorys*, *Histioneis*,

and *Ceratium ranipes*. Others are rather closely restricted to coastal waters and the neritic fauna, as, for example, *Exuviaella, Prorocentrum, Noctiluca,* and *Ceratium divaricatum.*

In view of the fact that representatives of this order have adapted themselves to salt, brackish and fresh waters and even to a parasitic mode of life, it is rather to be expected that they will be found in other available habitats as well.

The beach sands of the littoral zone offer such a habitat and one, moreover, which is constantly invaded by coastal waters laden with the neritic fauna. Whenever the tidal amplitude and the breakers come into play we find an automatic agency for the incessant stranding of the dinoflagellates of the neritic zone upon the surface and in the interstices of the beach sands. As each recurrent tide or breaker recedes the sand acts as a filter bed upon which is accumulated the plankton of the infiltrating water. This accumulating action of the beach sands is especially noticeable along the California coast whenever the outbreaks of "red water" due to dinoflagellates occur. At such times the beach becomes highly phosphorescent with its accumulating, but still living *Gonyaulax*, and becomes luminous whenever disturbed by the breakers or by passing footsteps.

A typical sand beach form is found in the genus *Amphidinium*, some of the members of which have not been recorded thus far from any other habitat. The occurrence of two or more species of this genus has been recorded by Herdman (1911, 1912, 1913), who followed for several years their recurrence on the beaches of the sheltered harbor at Port Erin, Isle of Man, in the Irish Sea. According to him, these species form a yellowish brown film, rippled by tidal movements, on the surface of the sands in April, September, October, and November, almost to the exclusion of diatoms, which abound at other times. These organisms were abundant from one day to two or even three weeks, after which they almost completely disappeared. Although abundant on the sands within tidal limits, these species could not be detected in the plankton of the immediately contiguous waters.

An examination of the arenaciphilous microfauna and flora at La Jolla also reveals a number of species which have not been observed in the hauls made concurrently a short distance offshore, nor have they been discovered in the pelagic collections made prior to or since these examinations. These examinations were made by rinsing the sands cautiously in fresh sea water, condensing the organism released thereby on filter paper, and examining the sediment thus collected. In addition to the representatives of the neritic plankton, of which a few stranded individuals were always present, there appeared to be an indigenous complex consisting of a few species of naviculoid diatoms, some small nematode worms and several species of dinoflagellates.

The dinoflagellates discovered in this complex were mainly members of the genus *Amphidinium*, as follows: *Amphidinium asymmetricum*, *A. corpulentum*,

*A. scissum, A. truncatum, A. dentatum,* with one representative each of the genera *Gymnodinium* and *Gyrodinium*, namely, *Gymnodinium hamulus* and *Gyrodinium viridescens.* We thus find the genus *Amphidinium,* previously reported from beach sands by Herdman, represented here by no less than five common species. It is also suggestive in its bearing on the isolation hypothesis that we find within this very restricted and fairly uniform habitat, in considerable abundance and constantly intermingled, five species of the genus *Amphidinium*, and, moreover, all these appear to be closely related, if structural similarity may be taken as a clue to relationship. These five species constitute nearly one-third of the valid species within the genus. A common habitat is no bar to speciation in this instance. It is also noteworthy that these sand beach forms present a type that is only rarely met with in the neritic and pelagic fauna, shown by the strong dorsoventral compression of the body.

The fresh-water species of the dinoflagellates also form another fairly uniform group, more nearly related to the arenaciphilous species than to either the neritic or pelagic forms. They are uniformly of a small size, with two exceptions, *Gymnodinium fuscum* and *G. mirabile*, which more closely approximate the average size among the pelagic group.

The fresh-water species of the Gymnodinioidae thus far described belong to the genera *Hemidinium*, *Amphidinium*, *Gymnodinium*, and *Gyrodinium*. Among the species of the last three genera found in this habitat there is a notable lack of the more highly specialized species, as well as a complete absence of the more highly developed genera of the Gymnodinioidae, the fresh-water forms representing only the more primitive and the more generalized species of the groups.

The non-thecate dinoflagellates are found in fresh water in all parts of the globe. Most of the species described, however, have been found in the central part of Europe, particularly in the waters of Switzerland and neighboring countries. Complete lists of these will be given in the further discussion of this subject under each genus and need not be repeated here.

From other parts of the world the records are only fragmentary. A single one comes from Egypt in the notes of Schmarda (1854), who records the presence of three species of *Peridinium* in the Nile River and adjacent waters. These are probably species of *Gymnodinium*. From South America the only representatives of this group of which we have any records are those of *Gymnodinium fuscum* and *G. viride* by Cunha (1913) from Brazil.

In North America a like paucity of observations on the Gymnodinioidae is found. Cockerell (1907–1910) noted the presence of an unidentified species of *Gymnodinium* in the waters at Boulder, Colorado. Conn (1905) also found a species of *Gymnodinium* in Connecticut. From Japan, Ohno (1911) has described a single species, *Gymnodinium biciliatum*, and from New Zealand Maskell (1887) reports *G. varians*. Three species of *Gymnodinium*, *G. aeruginosum*, *G. bogoriense*, and *G. varians*, were observed by Klebs (1912) in Java.

From the English, Scottish and Irish lakes, West and West (1909) record two species, *Gymnodinium paradoxum* and *G. zachariasi.*

These isolated references to the Gymnodinioidae in such widely separated waters indicate a wide range in their distribution which more complete investigations will undoubtedly greatly enlarge. They are among the smallest of the fresh-water fauna and hence easily escape observation.

In the marine group of the non-thecate dinoflagellates we find an equally wide distribution. From the colder waters of the Arctic Pouchet (1894) found *Gymnodinium wilczeki, G. pseudonoctiluca, Pouchetia polyphemus, Polykrikos schwartzi,* and *Gymnodinium* (=*Gyrodinium*) *crassum.* Meunier's work (1910) in the Arctic was more exhaustive, but together with the great number of other forms which he described he figures only three species belonging to this group, i.e., *Gyrodinium fusus, G. lachryma,* and *G. grave.*

The remainder of the members of this group, with one or two exceptions from tropical waters, are all found in the warm or cool temperate regions. Most of these come from the Atlantic or the bays along the west coast of Europe opening into it, including the Mediterranean. In a comparison of the lists of species given for these waters and the species found by us in the Pacific it is found that no great differences separate these two regions. Of the eighteen species of *Gymnodinium* previously described from this region of the Atlantic, seven have been found in the San Diego region; of the twenty-one species of *Gyrodinium,* six occur at San Diego; of the ten species of *Cochlodinium,* five are found at San Diego, and of the six species of *Pouchetia,* two are present in this region. This gives a total of fifty-five species of these four genera found in this region of the Old World, of which twenty have been identified by us in the San Diego waters, with a total of ninety-two new species present at the same place. The relative thoroughness of the exploration of these two regions and seasonal limitations of collections probably accounts for the disparity in these two series of numbers.

Kofoid (1910*a*) has pointed out the large proportion of the species of the thecate dinoflagellates described from other regions and present in the Pacific off San Diego. The relative proportions are somewhat greater than in the non-thecate forms. This may be due in part to the fact that observations on the thecate dinoflagellates have been carried on throughout the entire year for a number of succeeding years, while observations on the non-thecate forms have been limited to the months of June, July, and August. It may also be due to the greater knowledge generally of the thecate forms.

In regard to the seasonal distribution of the unarmored dinoflagellates but little can be said. Daily hauls have been made at La Jolla throughout the year, but only those of the summer months have been examined immediately after being taken. As the Gymnodinioidae cannot as a rule withstand the formalin used as fixative, the hauls so treated are useless for purposes of identification of this group, with very few exceptions. Our records, therefore, are complete only for the months of July and August.

Many species are apparently restricted in their seasonal appearance while others may be found at all seasons; for example, Lohmann (1908) records the presence of *Amphidinium crassum* and *A. rotundatum* in the Baltic Sea near Kiel, Germany, throughout the year. Other species have been recorded from two or more places in the same latitude and general temperature conditions for different months of the year, indicating a wide range of temperature relations.

It has been found in the thecate dinoflagellates, and it is probable that it is equally true here, that the period of greatest abundance, both specifically and numerically, extends from June to October or November. During the latter part of this period many tropical forms are found in the San Diego region, brought northward by the currents in the Pacific. At other times of the year drifters from the northern region are sometimes observed here. The occurrences of the latter species are influenced by the southbound California current from more northern waters.

One of the mysteries connected with the distribution of the dinoflagellates is the sudden occurrence of vast quantities of a single species, so great in amount as to give a distinct color to large areas of the sea. Such is the red water frequently noted in patches in the Pacific off the coast of California during the summer months. This is caused by *Gonyaulax polyhedra*, or in one case of red water at La Jolla in 1916 by *Prorocentrum micans*. In other localities species of *Ceratium* and *Peridinium* have been known to cause a distinct coloration of the water.

*Gymnodinium flavum* was the cause of an outbreak of yellow water at La Jolla during the summer of 1914. This was not very great in extent or serious in its results. This sudden appearance of vast numbers of a single species and an almost complete disappearance a few days later has no apparent relation to tides or currents. Its cause is probably a physiological one, and may be the response of a peculiarly susceptible organism to the stimulus of a sudden influx of materials present in their normal habitat in only limited quantities. The susceptibility of Dinoflagellata to extremely minute amounts of mineral substances is shown by the fact that one part in ten million by weight of copper sulphate is sufficient to kill off utterly within a few days all *Ceratium hirundinella* in California fresh-water reservoirs. The effect of this algicide is lasting, for months at least. It is theoretically possible that these may be not only growth depressants but excitants as well, the existence of which in minute quantities would suffice to set in motion and to continue such massive changes in production as appear in the red water, where the tonnage per acre is enormous. The possibility that such specific growth excitants exist among the *organic* substances accumulated by the processes of decay in the depths of the sea and near the light floor of the high seas is suggested by the fact that red water areas lie along our western coast where upwelling waters enrich the coastal region, and that the greatest abundance of the dinoflagellates, both of individuals and of species, in the ocean lies suggestively near the zone of initial decay of the phytoplankton.

Local Distribution.—The data for an adequate discussion of this phase of distribution of these pelagic organisms is wholly inadequate for two reasons. In the first place, there are no data from contiguous regions, and secondly, the species herein discussed were progressively discovered and allocated, so that within our own data the facts as to distribution are limited.

It will appear to the reader of the systematic section of this work that very few individuals have been seen of most of the species herein described, whereas the facts are that only those individuals are cited whose specific identity is recorded in drawings or was determined and recorded during the searching of the plankton. In the course of the investigation there were very many instances of species not recorded or not run down on the slide until sufficiently quiescent for certain identification.

The individuals of many of the species are in fact much more abundant than the data cited indicate.

The following conclusions as to local distribution are based on our observation and records: (1) The species are very unequally represented in numbers. Those which may be called common are relatively few. The following were common in the summer of 1917, or in previous years as noted, *Amphidinium truncatum* (1914), *Gymnodinium coeruleum* (1906), *G. costatum* (1917); *G. contractum*, *G. dogieli*, *G. flavum* (1914); *G. gracile*, *G. hamulus* (1914); *G. heterostriatum, G. lunula, G. rubricauda, G. rubrum, G. sphaericum, Gyrodinium maculatum, G. ochraceum, G. pingue, G. rubricaudatum, Cochlodinium citron, Torodinium teredo, Polykrikos kofoidi, Noctiluca scintillans, Nematodinium armatum* (1917). Thus 24 species out of a total of 116 are common, while 92 are rare, being represented in a number of instances by records of a single individual only.

(2) Species are not equally abundant in different years. Thus *Gymnodinium flavum* was very abundant in 1914, but in no other year. *G. coeruleum* was common in 1906, but not in 1917. *Polykrikos* appears to be rather common in most years.

(3) There is some evidence as to favored habitats. There is a distinct arenaciphilous fauna, which we have previously noted, adapted to that region. There are some species which survive in larger numbers than others in the immediately neritic waters, as shown in collections at the pier at La Jolla, but this is doubtless in part due to relative numbers, and may be, in part, the result of some vertical stratification.

(4) The region of greatest variety in species begins several miles offshore and is not in the innermost two to three miles. Many species found here occurred also at the pier, but less frequently and in much smaller numbers.

(5) The number of species taken in surface hauls from the upper two meters is much less than that taken in hauls from 80 meters to the surface. Hauls from greater depths do not materially increase the number of species found.

In our discussion of occurrences we have noted the depth from which the net was drawn in making the collection. The net was towed for about twenty minutes at the depth indicated, and then brought open to the surface. The organisms in the catch may have come from any level.

## HISTORICAL DISCUSSION

It is to the epoch-making work of O. F. Müller that we owe our first glimpse of the members of the dinoflagellate group. The first of these to be discovered were the fresh-water thecate forms of *Ceratium hirundinella* and a species of *Peridinium*. The former he called *Bursaria hirundinella* and the latter *Vorticella cincta* (1773). In a later work (1777) he records the discovery of a marine species also belonging to the genus *Ceratium*, as *Cercaria tripos*. The outlines of these forms were delineated with a fair degree of accuracy, but it was only in the species of *Peridinium* that the girdle was clearly marked.

Müller was followed by Schrank (1793), who established the genus *Ceratium* for a marine form which he designated *C. tetraceras*.

The most important of these earlier observations, however, were those of Michaelis (1830), who discovered that the phosphorescence of the sea was due, in a large measure, to these minute forms of animal life. He figured a number of species, among others *Prorocentrum micans*, which were later named by other investigators. He also was the first to observe the longitudinal flagellum, though mistaking the single one, with its constant activity in a cone-shaped amplitude of vibration, for several flagella.

In the same year appeared the first of a series of papers by Ehrenberg in which some attention was given to this group. Like his predecessors, the organisms which he observed were mainly those of the thecate forms. He described the genera *Prorocentrum*, *Glenodinium*, and *Peridinium*, describing under the latter designation species which were later removed to the genus *Ceratium*. In addition to these he described *Gymnodinium fuscum* as a species of *Peridinium*. He observed the flagella characteristic of the group, though figuring the ribbon-like transverse flagellum as a series of cilia. He also figured the girdle and sulcus.

The first attempt to form a systematic group of the dinoflagellates was also made by Ehrenberg (1830) in establishing the family Peridinaea for the genera *Peridinium* and *Glenodinium*, to which he later added the genus *Dinophysis*. This grouping was based on a recognition of the relations of flagella and girdles.

The genus *Prorocentrum* was not recognized by Ehrenberg as related to *Peridinium*, but was placed with the cryptomonads. His interpretation of the internal structures of these micro-organisms was in line with his conception of the Protozoa generally as more or less perfect miniature replicas of the Metazoa. Thus the vacuole he considered as a stomach, the chromatophores as ovaries, and the nucleus as a prostate gland.

It was also due to the indefatigable labors of Ehrenberg (1854) that the discovery of fossil dinoflagellates was made. These were mainly species of *Peridinium* present in the flints of Delitzsch, belonging to the Cretaceous.

The next landmark in the history of the dinoflagellates was the appearance of Stein's monograph in 1878. Between this date and the publication of the work of Ehrenberg a few contributions were made, chiefly on the thecate forms. Among these might be mentioned the investigations of Perty (1852) on the fresh-water species in the Alps and their environs. A few of the forms he described undoubtedly belong to the Gymnodinioidae, but considerable doubt attaches to them owing to the lack of adequate figures and descriptions. Also of interest from a geographical point of view is the work of Schmarda (1854) on forms from the Nile River and neighboring waters in Egypt.

Of more importance was the work of Claparède and Lachmann (1858–61), both from a developmental as well as a morphological viewpoint. They established the genus *Amphidinium* and recognized the dinoflagellate affinities of the genus *Prorocentrum*. They were the first to note the encysted forms, particularly the secondary, crescent-shaped cysts of at least two different species, one of which is undoubtedly *Gymnodinium lunula*. The flagellated organisms were oriented by these investigators, as well as by Ehrenberg, with the longitudinal flagellum projecting from the anterior end of the body—the reverse of its actual relations but in keeping with the conditions found among other flagellates. The transverse flagellum was also seen as a row of cilia extending around the body.

Claparède and Lachmann divided the Protozoa into four orders or tribes: Ciliata, Suctoria, Cilioflagellata, and Flagellata. The Cilioflagellata comprised the dinoflagellates and was based on their conception of the motor organelles of these forms as consisting of both cilia and flagella. This conception of the ciliate structure of the transverse flagellum was held by later investigators, as Stein (1878), Bergh (1881*b*), and Saville-Kent (1880–82), until the work of Klebs (1883) clearly pointed out the error of this interpretation.

With the appearance of Stein's monograph (1878–83) a new era of investigation on the flagellates was opened. In the twenty-five magnificent folio plates with which his work is illustrated we find the only accurate representation of the dinoflagellates that had been put forth up to this time. His figures were made with the high magnification of from 600 to 1200 diameters or more, hence his analysis of the finer structures as well as the organization of the body, gave an entirely new and adequate conception of these organisms, with the exception of the transverse flagellum, which he still figured as a row of cilia. His work is also notable for the number of new species which he added to the list of those previously described. He established the genera *Hemidinium* and *Gymnodinium* among the non-thecate forms, but the major part of his treatise relates to the thecate dinoflagellates.

Along with his clear interpretation of the organization of these flagellates he reversed the orientation used by earlier investigators and gave to the longitudinal flagellum a posterior trailing position. He also figured the oblique plane of division in the thecate group and division in encysted individuals of *Amphidinium*, without, however, noting the details of the division process.

The period following the publication of Stein's monograph was a more prolific one in the investigation of these organisms, both by the addition of new genera and species and by a more systematic classification of the group.

Bergh (1881*b*) divided the order Cilioflagellata into two families, the Adinida, containing *Prorocentrum*, and the Dinifera. The latter he divided into three subfamilies, the first, Dinophyida, containing *Dinophysis* and *Amphidinium*, the second, Peridinida, for *Peridinium* and related thecate species, and the third, Gymnodinida, for *Gymnodinium*, *Hemidinium*, and *Polykrikos*. He thus did not recognize the close relation of *Amphidinium* and *Gymnodinium*, but placed the former with the thecate genus, *Dinophysis*.

In 1880–1882 Saville-Kent put forth an extensive review of this group, adding two new species to the genus *Gymnodinium*. One of his most important observations was the discovery that these small *Gymnodinium* with which he was working were holozoic in nutrition. He also greatly enlarged the boundaries of the Cilioflagellata to include four families possessing both cilia and flagella, Heteromastigidae, Mallomonadidae, Stephanomonadidae, and Trichonemidae, which, he considered, intimately connected the Ciliata and Flagellata. These groups were later recognized as having affinities neither with the dinoflagellates nor with the ciliates.

The most noteworthy publication on this subject following Stein's was that of Bütschli in Bronn's *Klassen und Ordnungen des Thierreichs* in 1885. He pointed out the inadequacy of the earlier term Cilioflagellata and changed it to the more appropriate name Dinoflagellata, recognizing the true nature of the transverse flagellum, and gave an exhaustive review of the entire subject. He had earlier (1873) added the genus *Polykrikos* to the group, though in his first description of it he had described it as a ciliate infusorian. Bergh (1881*b*) placed it in the Cilioflagellata, and Bütschli accepted this allocation in his discussion of the Dinoflagellata.

Bütschli, as Bergh had done earlier, also disregarded the distinction between the thecate and non-thecate forms by placing *Gymnodinium* and *Peridinium* in one family, the Peridinida, *Amphidinium* with the Dinophysida, and creating a third family, Polydinida, for the genus *Polykrikos*.

Pouchet contributed a series of articles on the dinoflagellates from 1883 to 1894, based on studies at Concarneau, on the French coast, adding a number of new species to those already described. One of these was *Oodinium poucheti* (=*Gymnodinium pulvisculus*), parasitic on *Appendicularia*. The cycle of development which he described for this species was the first attempt as yet made to work out a complete life history of the dinoflagellates.

Pouchet's industry and his exceptional opportunities at Concarneau for studying the living dinoflagellates of the marine plankton greatly enlarged our knowledge of this group, especially of the unarmored forms. He added no less than fifteen species to the list. Unfortunately for the systematists who followed him, Pouchet's pioneer work was so fragmentary and his conception of specific limits so vague and changeable that his contributions are incorporated with difficulty in our present system. He added to our knowledge of *Polykrikos* and *Noctiluca*, but became involved in the latter's puzzling relations to "pseudonoctiluca" forms, without arriving at any clear conception of the relationships of *Noctiluca* to the dinoflagellates. His greatest contribution was his discovery of the ocellate forms which he included in *Gymnodinium*, but which now, as *Pouchetia*, bear his name. He also contributed to our knowledge of the arctic dinoflagellates in his account (1894) of the voyage of the "Manche" and of the relation of dinoflagellates to the food of the sardine.

Coincidentally with Pouchet's earliest work (1883) appeared Gourret's monograph (1883) on the Marseilles dinoflagellates. This also was a pioneer enterprise, and beyond recording a few new species and adding greatly to synonymical perplexities he contributed little to our permanent knowledge of the group. His conception of the phylogenetic position of *Gymnodinium* as a terminal derivative of the thecate *Glenodinium* and *Diplopsalis* is the reverse of what appears sound, and is on a par with his derivation of *Amphidinium* from *Dinophysis*.

The greatest single contribution made to this subject was that of Schütt, whose monograph on the dinoflagellates appeared in 1895 as part of the results of the "Plankton" Expedition. Both in the number and variety of forms which he figured and the careful and painstaking analysis of the structures and protoplasmic organization of these flagellates his work stands unrivaled. Seven of the large folio plates are devoted to the members of the Gymnodinioidae, adding many new forms to those previously described. He unfortunately omits all mention of the localities from which his material was obtained, hence his work has little to offer in the distributional and geographical study of the dinoflagellates.

In the following year (1896) the same author revised the system of classification of the dinoflagellates in Engler and Prantl's *Pflanzenfamilien*. He separated the thecate and non-thecate forms, and in the latter group distinguished the genera *Spirodinium* and *Cochlodinium*, with *Pouchetia*, a genus which he had established the preceding year. The entire group he divided into three divisions, the Gymnodiniaceae for the non-thecate forms, the Prorocentraceae and the Peridiniaceae for the thecate. With the Gymnodiniaceae he placed the genus *Pyrocystis*, which had been described by Murray in 1876. In thus recognizing the systematic value of the distinction between the thecate and non-thecate dinoflagellates he laid the basis of the present system of classification. Klebs (1912) returned to the older system in placing the genus *Amphidinium* in the Prorocentraceae. He also removed the thecate *Glenodinium*

from the group with which it naturally belongs, the Peridiniaceae, where it had been allocated by Schütt, and placed it in the Gymnodiniaceae. Having a distinct theca, it is sharply marked off from the dinoflagellates belonging to the Gymnodinioidae; and we therefore follow Schütt's allocation and reject it from that group.

Other reviews of this group have appeared in which no new contributions were made, such as those of Delage and Hèrouard (1896), Schönichen and Kalberlah (1900), and Paulsen (1908). Lemmermann (1910) included the Peridiniales in his work on the Algae, and in 1913 Schilling issued a monograph on the fresh-water dinoflagellates which, though short, is both comprehensive and accurate.

The single contribution of Dogiel (1906) is important in that he followed out the life history of two species of dinoflagellates, the free-living *Gymnodinium lunula*, and a species parasitic on copepod eggs, *Chytriodinium roseum* (*Gymnodinium roseum*). He also figured division in *Gymnodinium heterostriatum* (= *G. obtusum*), showing that this process follows an oblique plane similar to that found in the thecate dinoflagellates.

Our further knowledge of the parasitic dinoflagellates is due to the efforts of Chatton, who published a series of papers from 1906 to 1912 dealing with this highly interesting though small group.

The most illuminating and constructive treatment of the dinoflagellates, and one in which the unarmored types are adequately discussed, is that found in the chapter on Peridinieae in West's monograph (1916) on the *Algae* in the Cambridge Botanical Handbooks. Although of necessity brief, it is comprehensive and deals with the upstanding facts of the organization of this group in a masterly way. He correctly, in our view, places the Gymnodiniaceae near the base of his evolutionary scheme and independent of the Prorocentraceae, which he also places low in the scale. His derivation of *Dinophysis* from *Prorocentrum* seems to us less probable than one from an *Amphidinium*-like ancestor, and the inclusion of the Pyrocystaceae as an independent family we regard as untenable on the ground that *Pyrocystis* is, or will be found to be, a phase in the life history, a phase which, for a longer or shorter period, may be expected in most, if not all, free-living dinoflagellates. Furthermore, his conception of the Dinoflagellata as a group within which the distinctions between holozoic and holophytic nutrition have not become clearly established along definite systematic lines is eminently correct. We dissent, however, from his conclusion that "the saprophytic Peridinieae are probably mostly degenerate forms," and believe that the facts justify the conclusion that both saprophytic and holozoic nutrition play a much larger part in the evolution, past and present, of the Dinoflagellata, especially of the unarmored forms, than the evidence, heretofore at hand, has seemed to indicate. The estimate that "90 per cent of them are true vegetable organisms with a holophytic nutrition" may be true of fresh-water forms of the group with which the author is so familiar, but it certainly

can not apply to the Gymnodinioidae, nor to the deep-water, marine representatives where the saprophytic mode of nutrition tends to prevail.

Many other investigators have added details to our knowledge of the speciation, organization and geographical distribution of the non-thecate dinoflagellates, but further discussion of these will be reserved until the history of each group or species is taken up.

# CHAPTER IX

## CLASSIFICATION OF THE DINOFLAGELLATA

Regnum Animalia
  Phylum 1. Protozoa Goldfuss
    Superclass 1. Plasmodroma Doflein
      Class 1. Flagellata Cohn emend. Bütschli *sive*
        Mastigophora Diesing
        Subclass 1. Dinoflagellata Bütschli
          Order 1. Adiniferidea Kofoid and Swezy
            Tribe 1. Athecatoidae Kofoid and Swezy
                Genus 1. *Haplodinium* Klebs
            Tribe 2. Thecatoidae Kofoid and Swezy
              Family Prorocentridae Kofoid
          Order 2. Diniferidea Delage and Hèrouard emend.
            Tribe 3. Gymnodinioidae Poche emend.
              Family 1. Protodiniferidae Kofoid and Swezy
                Genus 1. *Protodinifer* Kofoid and Swezy
                  2. *Oxyrrhis* Dujardin
              Family 2. Gymnodiniidae Kofoid
                Genus 3. *Hemidinium* Stein
                  4. *Amphidinium* Claparède and Lachmann
                  5. *Gymnodinium* Stein emend.
                  6. *Gyrodinium* Kofoid and Swezy
                  7. *Cochlodinium* Schütt
                  8. *Torodinium* Kofoid and Swezy
              Family 3. Polykrikidae Kofoid and Swezy
                Genus 9. *Polykrikos* Bütschli emend.
              Family 4. Noctilucidae Saville-Kent
                Genus 10. *Pavillardia* Kofoid and Swezy
                  11. *Noctiluca* Suriray
              Family 5. Pouchetiidae Kofoid and Swezy
                Genus 12. *Protopsis* Kofoid and Swezy
                  13. *Nematodinium* Kofoid and Swezy
                  14. *Pouchetia* Schütt emend.
                  15. *Proterythropsis* Kofoid and Swezy
                  16. *Erythropsis* Hertwig

Family 6. Blastodiniidae Kofoid and Swezy
Genus 17. *Apodinium* Chatton
18. *Blastodinium* Chatton
19. *Chytriodinium* Chatton
20. *Ellobiopsis* Caullery
21. *Oodinium* Chatton
22. *Paradinium* Chatton
23. *Schizodinium* Chatton
24. *Syndinium* Chatton
25. *Trypanodinium* Chatton
Family 7. Cystodiniidae Kofoid and Swezy
Genus 26. *Cystodinium* Klebs
27. *Dinamoeba* Pascher
28. *Glenodinium* Klebs
Tribe 4. Amphilothioidae Kofoid and Swezy (doubtfully Dinoflagellata)
Family 8. Amphilothiidae Kofoid
Genus 29. *Amphilothus* (Schütt)
Family 9. Gymnasteriidae Poche (doubtfully Dinoflagellata)
Genus 30. *Gymnaster* Schütt
31. *Achradina* Lohman
32. *Monaster* Schütt
Tribe 5. Peridiniidae Kofoid and Swezy
Subclass 2. Cystoflagellata (Haeckel) emend., Kofoid and Swezy
Tribe 6. Cystoflagelloidae Kofoid and Swezy
Family 10. Leptodisciidae Kofoid
Genus 33. *Leptodiscus* Hertwig
34. *Craspedotella* Kofoid

## Subclass DINOFLAGELLATA Bütschli

Cilioflagellata Claparède and Lachmann (1858–61), pp. 72, 73, 392–412.
Cilioflagellata, Bergh (1881*b*), pp. 177–288.
Cilioflagellata, Saville-Kent (1880–82), pp. 439–469.
Arthrodele Flagellaten Stein (1883), pp. 1–30.
Dinoflagellata Bütschli (1885), pp. 906–1029.
Peridiniales Schütt (1896), pp. 1–30.
Dinoflagelliae Delage and Hèrouard (1896), pp. 373–388.
Peridiniaceae Schönichen and Kalberlah (1900), pp. 227–234.
Dinoflagellidia Kofoid (1907), p. 164.
Dinoflagellata, Doflein (1911), p. 325.
Dinoflagellata, Poche (1913), p. 160.
Dinoflagellatae Schilling (1913), pp. 1–64.

DIAGNOSIS.—Two flagella, one longitudinal, threadlike, usually posterior, trailing, the other ribbon-like and held transversely; girdle and sulcus more or less well developed; contractile vacuole absent; body either naked or covered with a sculptured shell. Colonial organization in ephemeral or permanent chain is sometimes found. The life cycle may show a greater or less extent of polymorphism.

This subclass contains 2 orders.

## KEY TO ORDERS OF THE DINOFLAGELLATA

1. Body either naked or with a bivalve shell, without well developed girdle or sulcus ........................ **Adiniferidea** nom. nov.

2. Body either naked or covered with a sculptured shell, girdle and sulcus present at some stage of the life cycle ........................ **Diniferidea** Delage and Hèrouard

## Order DINIFERIDEA Delage and Hèrouard emend.

Dinifera Bergh (1881*b*), p. 273. Family.
Diniferida Delage and Hèrouard (1896), p. 381.
Diniferida, Kofoid (1907*a*), p. 164.
Dinifera, Doflein (1911), p. 325.
Peridiniidea Poche (1913), p. 161. Suborder.

DIAGNOSIS.—This is a large group with a wide range of characteristics. The body may be naked or covered with a plain or sculptured shell or theca, continuous or composed of discrete plates; girdle and sulcus are well developed and always present at some period of the life cycle; nutrition may be holophytic, saprophytic, holozoic or parasitic; colorless to highly colored; ocelli and nematocysts sometimes present. The life cycle is usually complex, sometimes showing two distinct stages. Division is typically oblique. Sexual processes still obscure except in *Noctiluca*. Fresh water and marine. This order contains four tribes.

## KEY TO TRIBES OF DINIFERIDAE

1. Body naked, girdle and sulcus distinct at some period of the life cycle..**Gymnodinioidae** Poche

2. Body with superficial or more deeply embedded skeletal elements, without enveloping cuirass ........................ **Amphilothioidae** nom. nov.

3. Body naked without skeletal elements, girdle and sulcus suppressed ........................ **Cystoflagelloidae** nom. nov.

4. Body with theca composed of a continuous membrane or of discrete plates, epitheca and hypotheca separated by the girdle plates ........................ **Peridinioidae** nom. nov.

## Tribe 3. GYMNODINIOIDAE Poche emend.

Gymnodiniaceae Schütt (1896), p. 1.
Gymnodinina Kofoid (1907*a*), p. 164.
Gymnodiniaceae, Klebs (1912), pp. 438–443.
Gymnodinioidae Poche (1913), p. 161.
Kyrtodiniaceae Schilling (1913), p. 12.

Diagnosis.—Dinoflagellata with temporary or permanent longitudinal and transverse flagella, located respectively in sulcus and girdle; flagellar pore or pores ventral; cell body without a theca composed of discrete plates, naked or enclosed temporarily or constantly in a continuous, homogenous, gelatinous or cellulose cyst wall usually without a girdle. Fresh water and marine; holophytic, saprophytic, holozoic, or parasitic. This group contains 7 families and 30 genera.

### Discussion

This tribe as described by Poche (1913) contained two families, the Pyrocystidae and the Gymnodiniidae. The family Pyrocysteae was created by Schütt (1896) for the genus *Pyrocystis* Murray, to which he added, as *P. lunula*, the form he had described the year before as *Gymnodinium lunula*. Under the latter name encysted forms of various species of dinoflagellates have been figured as one species. A comparison of the figures of Pouchet (1885*a*, pl. 2, fig. 3), Schütt (1895, pl. 25, figs. $80_6$, $80_8$), Blackmann (1902, pl. 4), Wright (1906, pl. 1, figs. 3–6), Dogiel (1906, pl. 1), Okamura (1907, pl. 5, figs. 32*a-c*), and Apstein (1909, fig. 1) will plainly show that specific and even generic differences exist between some of the individuals thus figured. Schütt's figure $80_8$, plate 25, gives evidences of having a porulate theca.

We have pointed out elsewhere our views of the limitations of the species *Gymnodinium lunula* (p. 229). The allocation of the remaining members of the old genus *Pyrocystis* with their genetic relationships cannot be determined until their complete life histories have been investigated, since these are probably only phases of the life cycles of other dinoflagellates, both of the thecate and non-thecate types.

Klebs (1912) has further added to the confusion of this group of organisms. He changed the family Pyrocysteae Schütt to Phytodiniaceae, excluding from it the species *Gymnodinium lunula* (*Pyrocystis lunula* Schütt), and enlarged it to include four new genera, *Phytodinium, Tetradinium, Stylodinium,* and *Glocodinium*. The four new genera thus added may be dinoflagellates, but as they have been figured by Klebs they present none of the dinoflagellate characteristics and none of the characters of the genus *Pyrocystis* Murray except the outer wall. They seem more nearly related to the Conjugatae or Chlorophyceae than to the dinoflagellates as that group is at present constituted. Development

of these forms has not been followed out, neither have dinoflagellate stages been found. There seems to be, therefore, at present no reason for including them in the Dinoflagellata, though Poche (1913) recognized them as constituting part of the five valid genera in the family Pyrocystidae.

With the elimination of these genera proposed by Klebs, as not dinoflagellate in character, and the elimination of the genus *Pyrocystis* as composed of stages in the developmental cycle of other genera, there is no reason left for the continued existence of the family Pyrocystidae Poche, and we therefore discard it.

The second family of the Gymnodinioidae as established by Poche contains all the remainder of the non-thecate dinoflagellates. This is a large group and comprises within itself several smaller groups of closely related genera. The simplest of these forms is perhaps *Oxyrrhis* Dujardin. With its poorly developed girdle and sulcus it is not closely related to *Gymnodinium* or to other members of the Gymnodiniidae, but forms one of the connecting links between this family and the Adiniferidea. We therefore separate it from the Gymnodiniidae and place it in the family Protodiniferidae, together with *Protodinifer*.

A second natural grouping is found in those genera which possess an eyespot or ocellus. These represent a more advanced stage of development without closely intergrading forms between them and the *Gymnodinium* group. Hence the separation of these genera in a distinct family, the Pouchetiidae, seems appropriate both from a morphological as well as an evolutionary standpoint.

Still further removed from these three families is the group of parasitic genera. The acquisition of parasitism alone is not sufficient to separate a protozoan from the remainder of the forms to which it is closely bound by structural and developmental similarities. In the case of the parasitic dinoflagellates, however, this has resulted in profound modifications of the structure of the body as well as in its development. These seem to be sufficient to mark off the genera thus characterized as a separate family. To that end the family Blastodiniidae has been formed for the parasitic dinoflagellates.

Equally distinct from a morphological viewpoint are those dinoflagellates which have a well developed tentacle. To this group belongs *Noctiluca,* which has heretofore been placed in the Cystoflagellata Haeckel. The discovery of the genus *Pavillardia*, with its well developed girdle and sulcus as well as tentacle, and of *Erythropsis* with a still further development of the tentacular region into a prod with protractor and retractor fibrillae, bridges the gap which had earlier separated *Noctiluca* from the remainder of the dinoflagellates. Two of these genera fall within different families; *Protodinifer,* as one of the simpler, is referred to the Protodiniferidae, and *Erythropsis* to the family Pouchetiidae because of its ocellus. This leaves the two remaining genera, *Pavillardia* and *Noctiluca,* in the family Noctilucidae Saville-Kent.

The genera *Phytodinium, Tetradinium, Stylodinium,* and *Gloeodinium,* erected by Klebs (1912), are excluded by us from the Gymnodinioidae. There is considerable doubt in our minds as to their close relationship with the

Dinoflagellata. Pending the demonstration that they have in their life cycle a true dinoflagellate phase it seems best to hold them in suspense. We have accordingly omitted detailed treatment of this family in this monograph.

The genera *Cystodinium* and *Hypnodinium* of Klebs (1912) appear to share with *Glenodinium* the peculiarity of having a thin structureless theca closely adherent to the cytoplasm in the free stage where known. We therefore exclude them from the Gymnodinioidae and from this monograph.

## Key to the Families of the Tribe GYMNODINIOIDAE

1. Girdle and sulcus feebly developed, both flagella nearly threadlike, not parasitic, no tentacle, no ocellus, no cell membrane, not permanently colonial .................................................. **Protodiniferidae** fam. nov.

1. Girdle and sulcus well developed, transverse flagellum ribbon-like, permanently colonial 2

2. Not permanently colonial .................................................. 3

2. Permanently colonial, with nematocysts .................................................. **Polykrikidae** fam. nov.

3. No ocellus .................................................. 4

3. Ocellus present .................................................. **Pouchetiidae** fam. nov.

4. No tentacle .................................................. 5

4. Tentacle present, no ocellus .................................................. **Noctilucidae** fam. nov.

5. Not parasitic .................................................. **Gymnodiniidae** Poche

5. Parasitic at some stage .................................................. **Blastodiniidae** fam. nov.

## Family 1. **PROTODINIFERIDAE** fam. nov.

Diagnosis.—Gymnodinioidae with rudimentary girdle and sulcus; flagella anterior or ventral; ocellus lacking; tentacle more or less well developed. Length, $10\mu$ to $50\mu$. Marine; neritic from warm temperate waters; 2 genera.

Description.—This family contains representatives of the most primitive Gymnodinioidae and forms a connecting link between the Diniferidae and the Adiniferidae. The rudimentary girdle and sulcus and the anterior or ventrolateral position of the flagella, as distinct from the entire absence of girdle and sulcus and the anterior position of the flagella in the Adiniferidae, links this family with the Diniferidae rather than with the more primitive Adiniferidae.

In the development of the girdle and sulcus in this family two distinct stages are present. In *Protodinifer* these structures are found as the merest rudiments anteriorly located, with the girdle less than one-half the circumference of the body in length and faintly outlined. In *Oxyrrhis* the girdle or groove is ventrolateral and extends nearly or quite around the body, with a well defined border on the anterior margin, the posterior one sloping away to the narrowed posterior region of the body. In *Protodinifer* a tentacle springs from the sulcal region and extends anteriorly some distance beyond the apex of the body. In *Oxyrrhis* the tentacle-like projection also arises from the sulcal area in the region of the two flagellar pores, but its length seldom exceeds one-half the distance between the pores and the antapex. It also appears to be attached to the sulcal area for part of its length. The origin and position of the two structures are essentially the same in both genera.

The body is asymmetrical with no appreciable torsion in either genus. The nucleus is generally found near the center of the body with its chromatin contents arranged in characteristic moniliform strands. Nutrition is holozoic or saprophytic.

This family contains two genera, *Protodinifer* and *Oxyrrhis,* with a single species in each.

### Key to Genera of **Protodiniferidae**

1. Girdle short, faintly outlined, tentacle long, flagella anterior ................**Protodinifer** gen. nov.

2. Girdle nearly or quite 1 circumference in length, tentacle short, flagella ventrolateral ............ ..................................................**Oxyrrhis** Dujardin

## **PROTODINIFER** gen. nov.

Plate 7, figure 74; text figure R, 2

Diagnosis.—Protodiniferidae with anteroventral tentacle and sulcus, feebly developed anteriorly located girdle, long threadlike transverse and short longitudinal flagellum; no lens or pigment; no large hydrostatic vacuoles, small flagellates, marine.

This genus contains two species, both marine, *Protodinifer tentaculatum* sp. nov., the type species of the genus, and *P. marinum* (Lohmann). The latter is provisionally transferred here from *Rhynchomonas* on the basis of its morphological features other than the very essential primitive girdle and sulcus and the beaded chromatin in the nucleus, features which are as yet undetermined in this species.

The genus *Rhynchomonas* Klebs is based on a species (*R. nasuta*) from fresh water whose nucleus is of the vesicular type. This flagellate has an asymmetrical proboscis-like tentacle and a trailing flagellum. It thus superficially resembles *Protodinifer,* whose relationships to the Dinoflagellata are revealed by its nucleus with its moniliform chromatin network.

### Key to the Species of **Protodinifer**

Tentacle stout, length of body 54$\mu$ ..................**tentaculatum** sp. nov.

Tentacle slender, length of body 12–40$\mu$ ..................**marinum** (Lohmann)

### **Protodinifer tentaculatum** sp. nov.

Plate 7, figure 74; text figure R, 2

Diagnosis.—A small species with fusiform body, its length 2.45 transdiameters; girdle near apex, feebly developed and evanescent; sulcus scarcely evident; longitudinal flagellum short; apex modified in the form of a stout mobile tentacle 0.22 of length of body in length; color greenish grey to pale ochraceous. Length 54$\mu$. Pacific off La Jolla, California, July, August.

DESCRIPTION.—The body is stout fusiform, widest posteriorly, apex acuminate, tapering somewhat anteriorly, its length, including the tentacle, 3.8 transdiameters at the girdle. It is subcircular in cross-section but flattened somewhat ventrally in the anterior half. The hypocone is 3.3 transdiameters in length or 7 times the length of the epicone. The antapex is contracted to a stout subconical or slender acuminate horn 0.5 to 1 transdiameter in height. The epicone is comparatively minute, about 0.5 transdiameter at the girdle in height, subconical with convex sides and blunt antapex, which in one case was slightly bifurcated without any accompanying evidences of mitosis.

The girdle is rudimentary, scarcely visible, and in individuals from collections which have stood for some hours in the laboratory it wholly disappears. It is located far anteriorly at 0.15 of the total length of the body from the apex. It lies in a transverse plane and is developed from the pore of the transverse flagellum distally only about 0.25 of the circumference. It is the merest shallow rounded trough, without marked lips, ridges or list of any sort. The transverse flagellum lies habitually in this girdle and continues in its plane to encircle the body. Its full length completely encircles the body, though its distal end is sometimes spasmodically thrown anteriorly and brought back into place. As the animal grows moribund this flagellum falls away from its habitual position as in other dinoflagellates. It is a very narrow ribbon with well marked basal axis and characteristic short undulations which travel incessantly towards its distal end.

The fully developed sulcus runs from the flagellar pore anteriorly to the apex as a rather deep trough, sometimes laterally overhung by the edges. It is straight, shows no separate pore for the longitudinal flagellum and encloses the base of the stout tentacle, which merges into its dorsal wall. A denser tract passes posteriorly for a short distance into the cytoplasm from its base. The sulcus does not extend posteriorly upon the hypocone.

The longitudinal flagellum of this species has been reduced to a short lash, and in its place an anteriorly directed tentacle has been developed, which is the most striking characteristic of the organism. This is a stout rodlike structure projecting about 0.25 of the length of the body beyond the apex. It is cylindrical, of equal caliber throughout and terminates bluntly in a squarish tip. A differentiated axial core of greater density traverses its entire length.

The cell contents consist of a very indistinct nucleus located in the anterior half of the body and food masses. The nucleus is ellipsoidal in form with its major axis running from the right anteriorly to the left posteriorly. It is traversed longitudinally by coarse, nodulated chromatin threads, about ten on one face. Posterior to this, and filling the posterior half of the hypocone, is a large, subspheroidal, dull orange-yellow food body with several adjacent smaller spheres. In some individuals this is broken up into a number of smaller spherules. In still others a cloud of small, rounded, elliptical, or rodlike, dark olive granules surrounds the anterior half of a food body in a broad irregular band. A cluster of highly refractive, spherical oil droplets fills the antapical cone and several linear greenish rodlets, or a single large stout one, lie near the flagellar pore. The pinkish pusule lies posterior to the pore in the median line and is connected with the pore by a slender canal. The general color of the cytoplasm is a greenish grey, with a yellowish or ochraceous tone anteriorly. There are no striae on the surface and no scattered vacuoles or droplets of pigment.

DIMENSIONS.—Length, $54\mu$; transdiameter, at the girdle, $13\mu$, at the widest part of the hypocone, $23\mu$; length of tentacle beyond the apex, $16\mu$.

VARIATION.—The principal variations noted are due to the size of the ingested food bodies. When this is large the posterior third is somewhat distended In one case the antapex was much more acuminate than in the others. It is not metabolic to any considerable degree, the only changes of this sort noted being a tendency to form a constricted ring around the base of the tentacle.

Occurrence.—Described from four individuals taken in a plankton haul made with a No. 12 silk net from forty fathoms, six miles off La Jolla, California, in the California Current, July 2, 1917, in surface temperature of 21°95 C. It was observed also on July 20, 6 miles offshore, July 25, 11 miles offshore, July 27, 4 miles offshore, and August 13, 0.75 mile offshore, in surface temperature varying from 21°95 to 22°45. It was also taken on July 12 and 20, 1906, in surface hauls off La Jolla made between 5 and 6 a.m.

Activities.—The tentacle is habitually held in a somewhat rigid position, directed anteriorly, with a slight dorsal curvature. In moribund individuals it is gently waved to and fro in a short arc intermittently. When in a more active condition the flagellum is energetically raised to the horizontal plane and thrust back in a quick stroke which drives the animal backward with a sudden dart.

The behavior of the animal under the cover glass is generally, however, of a somewhat different nature. It moves with little rotation in a clockwise spiral anteriorly for short periods intermittently, with an occasional dart posteriorly. This posterior movement is an unusual one among dinoflagellates, and there seems to be no other motor organ than the tentacle to accomplish it. The suppression of the function of rotation may be due to the imperfect girdle and the varying position of the transverse flagellum.

Comparisons.—This genus is unique among the tentacle-bearing dinoflagellates in the anterior position of the girdle, and in the exceedingly rudimentary stage of development of this characteristic feature of the order. In *Erythropsis agilis* Hertwig the girdle is as well developed as in *Pouchetia*, and the tentacle or prod is relatively very much larger. In addition this genus is provided with a prominent lens and pigment mass. In *Pavillardia tentaculifera* the tentacle is quite similar in size and shape to that in *Protodinifer*, but it is colored a brilliant brown, as is the pigment in *Pouchetia rosea*, and the girdle and longitudinal furrow are of the *Gyrodinium* type. In *Gymnodinium pseudonoctiluca* the girdle is complete and located far anterior and the tentacle is proportionately longer than in *Protodinifer*.

From these comparisons it is evident that the genus is not closely affiliated with any of the other tentaculate dinoflagellates. It resembles *Hemidinium* and *Noctiluca* in the incompleteness of the girdle, but the former is an isolated fresh-water genus in which little speciation has occurred, while this one feature exhausts its resemblances to *Noctiluca*. The simplicity of structure places *Protodinifer* at the lowest level of the tentacle-bearing dinoflagellates. The anterior position of the flagellar pore and the very slight differentiation of the two flagella, the proportions of the body and the coloration are strongly suggestive of a relationship to *Prorocentrum*. It lacks, however, all trace of a theca and must be regarded as an athecate representative of the Diniferidae of primitive type from which the Adiniferidae are an offshoot. The feebly developed sulcus and girdle are indicative of tendencies which, if accentuated,

would lead to the higher Diniferidae. It forms a connecting link between the Adiniferidea and the Diniferidea and supports the monophyletic origin of the Dinoflagellata.

### **Protodinifer marinum** (Lohmann) Kofoid and Swezy

*Rhynchomonas marina* Lohmann (1902), pp. 7, 48, pl. 2, figs. 42–45; (1909), p. 223, fig. 4, nos. 36, 37.

*R. marina,* Lühe (1913), p. 261, fig. 266.

Diagnosis.—Elongate fusiform or pyriform, length 2.6 diameters, tentacle slender, 0.25 length of body in length; length, 12–40μ. Marine.

Description.—Lohmann (1902) gives a brief description and a few incomplete figures which afford the basis for the following account. Body fusiform in free state, length 2.1–2.6 times greatest diameter which may be equatorial or in the posterior third of the body. A tendency to become pyriform and enlarged posteriorly is seen in the smaller individual and in encysted and contracted stages. No trace of a girdle was figured or recorded. The slender tentacle is in all cases figured as terminal and no sulcus is clearly shown. Only a single posteriorly directed flagellum is figured. This is nearly 1.4 the length of the body in length. In the so-called young stage the tentacle is figured as stout, much like that in *P. tentaculatum.* No nucleus is described, but a spheroidal yellow body quite similar to that in *P. tentaculatum* is located posteriorly. A few large refractive spherules occur in the rounded antapical region and a cluster of smaller refractive corpuscles lie anterior to the yellow body. A flask-shaped pusule is found near the anterior end of the body.

Encystment occurs with the formation of a thin, closely adherent membrane from which the tentacle protrudes. The cyst later expands into a sphere and the body takes on a stout pyriform shape within it.

Dimensions.—Length, 12 to 40μ; greatest diameter, 5 to 17μ; tentacle, 2 to 10μ.

Occurrence.—Reported by Lohmann (1902) from the plankton in the Bay of Kiel and later in 1909 in the food contents of the digestive tract of *Appendicularia* from the Baltic and Mediterranean seas, but not explicitly from the latter.

Comparisons.—This species differs from *P. tentaculatum* mainly in size. It ranges from 12 to 40μ, while the specimens of the former species are 54μ in length. The tentacle also appears to be more slender and to be terminal, but Lohmann's figures may not be critical on this point. It also has a body of a more slender type and a longer transverse flagellum. Lohmann does not figure the minute longitudinal flagellum if there be one. The resemblance to *Protodinifer* is so striking that we are led to transfer the species from *Rhynchomonas,* where Lohmann placed it, to *Protodinifer* in the face of the facts that that author did not note any trace of a girdle, any longitudinal flagellum, or any nucleus. This may prove to be of the dinoflagellate type with beaded chromatin. We saw no individuals of *P. tentaculatum* with the very slender tentacle which Lohmann figures for this species. The two species are close together and may prove to be identical. However, with our present knowledge, the differences in size, tentacle, and flagellum are such as to lead to specific separation.

Synonymy.—Lohmann originally described this species as *Rhynchomonas marina*. However, *R. nasuta*, the type species of Kleb's genus *Rhynchomonas* (1892), does not have the beaded chromatin nucleus characteristic of the Dinoflagellata, as shown by the investigations of Belar (1915), nor are the tentacles of the two species, *R. nasuta* and *R. marina*, as nearly alike as those of *Protodinifer tentaculatum* and *P. marinum*. We do not know the nuclear structure of Lohmann's species. We assume on the basis of the other morphological features that it will prove to be of the dinoflagellate type and make the generic transfer thereon to *Protodinifer*. If it does not have such a nucleus it should not be transferred here.

## OXYRRHIS Dujardin

Text figure R, 3

*Oxyrrhis* Dujardin (1841), pp. 346, 347, pl. 5, fig. 4.
*Oxyrrhis*, Diesing (1850), p. 58; (1865), p. 79.
*Glyphidium* Fresenius (1865), pp. 83, 84, figs. 4–10.
*Glyphidium*, Cohn (1866), pp. 295, 296, pl. 15, figs. 36, 37.
*Oxyrrhis*, Saville-Kent (1880–82), pp. 426–428, pl. 24, figs. 53–61.
*Oxyrrhis*, Bütschli (1885), p. 845, pl. 45, fig. 12.
*Oxyrrhis*, Senn (1900), pp. 136, 137, fig. 93; (1911), pp. 606–643, pl. 35, figs. 1–4.

Diagnosis.—Body subovoidal, asymmetrically contracted on the left posteriorly; girdle postmedian, incomplete distally, lacking postmargin; sulcus spreading posteroventrally, divided anteriorly by pendant tentacular lobe; transverse flagellum originating to the left and the longitudinal to the right of the lobe; nucleus with beaded chromatin; marine.

Relationships.—The nuclear structure with its very characteristic beaded chromatin, clearly demonstrated in the researches of Keysselitz (1908) and Senn (1909), establishes beyond question the dinoflagellate affinities of this puzzling flagellate. The oblique (almost transverse) fission, the subsequent chain formation by the two schizonts, the posteriorly directed longitudinal flagellum, and the partially developed girdle support this interpretation. There is need of further research on the structure and behavior of the transverse flagellum and of the tentacular lobe.

The dinoflagellate affinities of *Oxyrrhis* have been pointed out by Senn (1909*a*, *b*) on the basis of the nuclear structure and general morphology, and by Jollos (1910) on the ground of the nucleus alone. This relationship was first suggested, however, by Bütschli (1885), who called attention to the fact that *Oxyrrhis* had the dinoflagellate type of nucleus and posteriorly directed flagella. He also noted the difference between the two flagella and concluded that *Oxyrrhis* might be regarded as a form intermediate between the Cryptomonadina on the one hand and the Dinoflagellata (*Hemidinium*) on the other. Unfortunately this view had not been incorporated in his earlier (1885) monograph where *Oxyrrhis* was included in the Cryptomonadina. Delage and

Hèrouard (1896) assigned it to the Heteromastigina and Senn (1900), in his earlier monograph of the flagellates, placed it in the Bodonaceae. Poche (1913) does not allocate it in his "System der Protozoa."

The grounds upon which *Oxyrrhis* may be considered a primitive dinoflagellate are its imperfect girdle and its apparent lack of differentiation of the transverse flagellum into the typical ribbon. The sulcus appears to be incompletely differentiated. The tentacular lobe, however, is a specialized rather than a primitive feature. It appears to be homologous with the tentacle of *Protodinifer.*

The fact that the thecate genus *Prorocentrum* of the Adiniferidea also has a projection near the flagellar pore is significant, especially if this group is an offshoot from lower Diniferidea of which *Protodinifer* and *Oxyrrhis* are the existing representatives. The fact that the tentacle in these two genera is a mobile organ and the projection of *Prorocentrum,* an immobile part of the exoskeleton, need not militate against the homology, for the somewhat mobile girdle of *Gymnodinium* is certainly homologous with the zone of girdle plates in the Peridinioidea. In view of the form and location of this projection in *Prorocentrum* it appears that *Protodinifer* is nearer the Adiniferidea than is *Oxyrrhis,* which, in the location and imperfection of the girdle, is much nearer *Hemidinium* than is *Protodinifer. Oxyrrhis* may then be regarded as a more specialized and higher representative of the Protodiniferidae than is *Protodinifer.*

*Oxyrrhis marina* appears to be the only valid species in the genus. Poche (1903) described *O. parasitica* from the coelenteron of the Siphonophora. It is a minute flagellate with two unequal flagella in the midventral surface. There is no other evidence of its affinities to *Oxyrrhis.* We therefore agree with Senn (1911) in excluding it from that genus, pending investigation of its nucleus and flagella. Scherffel (1900) described another parasitic flagellate living in the coenobia of *Phaeocystis globosa,* which he called *Oxyrrhis phaeocysticola.* There is no evidence of a girdle or of a beaded nucleus in his account or in his figures of this species. There are suggestions in the shape, posterior brown body, and anterior tentacle-like projection, of relationships to *Protodinifer,* but more investigation is needed before a decision can be made regarding its true affinities. It does not appear to be an *Oxyrrhis.*

### **Oxyrrhis marina** Dujardin

Text figure R, 3

*Oxyrrhis marina* Dujardin (1841), p. 347, pl. 5, fig. 4.
*O. marina,* Diesing (1850), p. 57; (1865), p. 79.
*Glyphidium marinum* Fresenius (1865), pp. 83, 84, figs. 4–10.
*G. marinum,* Cohn (1866), pp. 295, 296, pl. 15, figs. 36, 37.
*Oxyrrhis marina,* Cienkowsky (1881), pp. 130–171, figs. 1–3.

*O. marina,* Saville-Kent (1880–82), pp. 427, 428, pl. 24, figs. 53, 61.
*O. marina,* Gruber (184), p. 417.
*O. marina,* Blochmann (1884), pp. 46–49, pl. 2, figs. 14–21.
*O. marina,* Bütschli (1885*a*), p. 845, pl. 45, fig. 12; (1885*b*), pp. 558, 559, figs. 1, 2.
*O. marina,* Stepanoff (1885).
*O. marina,* Gourret and Roeser (1886), pp. 448, 522–524, pl. 34, figs. 11–19.
*O. marina,* Delage and Hèrouard (1896), pp. 306, 314, 336, fig. 533.
*O. marina,* Entz (1897), pp. 177, 181; (1901), pp. 96, 98.
*O. marina,* Senn (1900), p. 137, fig. 93; (1909), pp. 85–87; (1911), pp. 605–672, pl. 30, text figs. 1–7.
*O. marina,* Scherffel (1900), p. 3.
*O. marina,* Massart (1901), p. 81.
*O. marina,* Lang (1901), p. 171; (1913), p. 231, fig. 232.
*O. marina,* Keysselitz (1908), pp. 334–339, pl. 19.
*O.* [*marina*], Willey and Hickson (1909), p. 184, fig. 102.
*O. marina,* Günther (1911), p. 9.
*O. marina,* Doflein (1911), p. 529.
*O. marina,* Minchin (1912), p. 278, fig. 123.
*O. marina,* Griessmann (1913), pp. 3, 14.
*O. marina,* Lebour (1917*a*), p. 154; (1917*b*), pp. 198, 199.

DIAGNOSIS.—Body elongate oval, asymmetrical posteriorly; girdle imperfect on right side, without a postmargin; flagella midventral; stout tentacle-like lobe pendant between the two flagella, dividing the broad undeveloped ventral sulcus; colorless; length, 10–37$\mu$. Marine.

DESCRIPTION.—The body is elongate oval, widest at the girdle, its length 2.25 transdiameters, and 2.6–3.2 dorsoventral diameter. The epicone is ovoidal, apex broadly rounded, over twice the size of the hypocone; its length at the origin of the transverse flagellum is about 0.5 total length, and at the left margin of the body about 0.75 total length. The hypocone is about 0.5–0.7 the diameter of the epicone and 0.5–0.25 the total length in length, tapering conical, displaced to the left, deficient on the right. It is broadly and deeply excavated ventrally. The antapex is bluntly rounded.

The girdle is peculiarly modified. It is incomplete, making about 0.75 of a circuit, fading out on the right side of the body. The anterior lip is a sharply overhanging shelf, but the posterior is lacking. Beginning in the midventral region, at the proximal end of the transverse flagellum the girdle drops obliquely posteriorly to the left margin of the body about half way to the antapex and continues thence transversely across the dorsal surface to the right side, where it vanishes. The sulcus is a broad excavation spreading over a considerable part of the ventral surface of the hypocone. It is divided in the median line by the pendant, tentacle-like lobe which separates two flagellar pores. This lobe is pear-shaped in outline, is half as long as the hypocone, and is attached by its stem between the two flagella to the anterior lip of the girdle and by its dorsal face to the hypocone. It may be extended as a more slender tentacle. It does not appear to be a modified flagellum.

The longitudinal flagellum originates on the right side of this lobe and the transverse one on the left. The former may extend directly posteriorly or it may wrap itself around the lobe, turning first anteriorly to the pore of the transverse flagellum and projecting posteriorly from that region, according to Senn (1911). There is a blepharoplast at the base of each flagellum. The transverse flagellum is about as long as the girdle, and is thrown into short undulations or a close spiral coil, but is not figured as a ribbon by Senn (1911), in which form it occurs in other dinoflagellates.

The cytoplasm is colorless, with a peripheral layer of stout rhabdosomes, 0.3 transdiameter in length. The nucleus lies in the lower epicone. It is an ellipsoid, 0.66 transdiameter in length and 0.50 in width, with about twelve moniliform chromatin threads on one face and a central nucleolus.

Binary fission is slightly oblique and the daughter cells form in chains as in other dinoflagellates.

DIMENSIONS.—Length, 22–32$\mu$, rarely 10–37$\mu$; transdiameter, 15–20$\mu$.

OCCURRENCE.—This species was originally described by Dujardin (1841) in salt water from the Mediterranean containing *Ulva* which had stood for some months. In fact most of the studies of this interesting and perplexing flagellate have been made from aquarium cultures. The only reports of the occurrence of the species from marine waters are those of Saville-Kent (1880–82), who found it in water samples from St. Heliers, Jersey, as well as in aquarium cultures from this region; of Cienkowsky (1881), who reported it from the White Sea; of Gruber (1884), who listed it from the harbor at Genoa, Italy; of Gourret and Roeser (1886), who found it sparingly in harbor water at Marseilles, France; of Massart, who collected it on brackish-water pools at Palingbrug, near Nieuport, Belgium; of Entz (1897), who discovered it in collections from brackish-water pools on a coral islet at Tengeriek, New Guinea; of Lohmann (1909), who records it from the harbor waters at Kiel; and Lebour (1917*a*, *b*), who found it sparingly in water samples at Plymouth, England.

On the other hand, it has been reported in great abundance in sea water aquaria at Frankfort, Germany, by Fresenius, who called it *Glyphidium marinum*. It was again found by Cohn (1865), who gave it this same name, in a window aquarium at Breslau supplied from Helgoland. Blochmann's (1884) studies were made on material from the Heidelberg Aquarium; Senn (1909) at Basel, Switzerland, noted it in great abundance in a culture from Naples containing *Bryopsis*, kept at 20° to 25° and not fouled by bacteria, flagellates, and ciliates. Griessmann noted its occurrence in aquaria supplied with sea water and seaweeds from Roscoff, Helgoland, and Villefranche. Lebour (1917*b*) reports it in great abundance in laboratory plankton cultures, especially with the diatom *Nitzschia closterium*.

Of special interest is its occurrence in continental salt lakes of the province of Kharkoff, Russia, reported by Stepanoff (1885).

SYNONYMY.—There is no doubt that the organism described by Fresenius (1865) as *Glyphidium marinum*, and later reported by Cohn (1886), is Dujardin's *Oxyrrhis marina*. The peculiar location of the flagella and their posterior position in locomotion, coupled with Dujardin's (1841) noncommittal horizontal orientation of his figures, misled these earlier investigators in their conclusions.

## CHAPTER X

# GYMNODINIIDAE: HEMIDINIUM, AMPHIDINIUM

## Family 2. **GYMNODINIIDAE** Kofoid

Gymnodinida Bergh (1881*b*), p. 274. Subfamily.
Gymnodinieae, Schütt (1896), p. 3.
Amphidinieae Schönichen and Kalberlah (1900), p. 229.
Gymnodinidae Kofoid (1907*a*), p. 164; (1907*b*), p. 293.
Gymnodiniidae, Poche (1913), p. 162.
Kyrtodiniaceae Schilling (1913), p. 12.

Diagnosis.—Gymnodinioidae with girdle varying in length from 0.5 to 4 turns around the body; sulcus extending from near apex to near antapex; ocellus and tentacle lacking; pusules usually present; plasma may contain chromatophores, colored pigment or be itself highly colored. Length, 11 to 221$\mu$. They are found in both fresh and salt water, are eupelagic, neritic or littoral, and occur in arctic, cool and warm temperate and tropical waters.

Description.—The members of this family show a progressive differentiation of the body as shown in the length of the girdle and the torsion of the body resulting therefrom. Both sulcus and girdle are well developed, the latter varying in length from 0.5 to 4 turns around the body, with a corresponding lengthening of the sulcus. With the increasing torsion of the body the length of the sulcus increases mainly in the intercingular area, rarely showing apical or antapical loops. The nucleus generally lies near the center of the body and may or may not have a perinuclear membrane. Its chromatin contents are always arranged in characteristic long, moniliform chromatin strands. Pusules are usually present, opening anteriorly into the anterior and posteriorly into the posterior flagellar pore, or both may be connected by a slender canal, forming a complete channel between the two openings.

The plasma may be highly colored and frequently contains colored pigment. Chromatophores are found quite generally in the fresh-water forms, more rarely in the marine species, occurring in *Amphidinium, Gymnodinium,* and *Gyrodinium.* Nutrition is both holozoic and holophytic, and apparently both phases may be assumed in the same species; individuals occasionally met exhibited both chromatophores and food bodies in the cytoplasm at the same time.

The cytoplasm may show a differentiation into ectoplasm and endoplasm or the former may consist only of a thin periplast. Longitudinal striae on the surface of the body are frequent. Cyst formation is frequent, either as the result of the ingestion of large food bodies or as division cysts. It is secreted by the body as a closely adherent membrane, which becomes distended by gradually accumulated fluid between itself and the body.

This family contains 6 genera: *Hemidinium,* with 2 species; *Amphidinium,* 22; *Gymnodinium,* 76; *Gyrodinium,* 47; *Cochlodinium,* 29; and *Torodinium,* 2, giving a total of 178 species. They form one of the most closely intergrading groups in the Dinoflagellata, with clearly established lines of relationship and evolutionary development.

We add to this family two new genera, *Gyrodinium* and *Torodinium,* and 92 new species distributed among the genera as follows: To *Amphidinium,* 12 new species; to *Gymnodinium,* 36; to *Gyrodinium,* 21; to *Cochlodinium,* 21; and to *Torodinium,* 1.

### KEY TO THE GENERA OF THE FAMILY **Gymnodiniidae**

1. Girdle of 0.5 turn only ........................ **Hemidinium** Stein
2. Girdle anterior, epicone relatively minute ........................ **Amphidinium** Clap. and Lach.
3. Girdle submedian, displaced less than 0.2 total length of body ........................ **Gymnodinium** Stein
4. Girdle posterior, without displacement, sulcus with long apical loop...... **Torodinium** gen. nov.
5. Girdle displaced 0.2 or more of total length of body with torsion of 1 to less than 1.5 turns.... ........................ **Gyrodinium** nom. sp. nov.
6. Girdle with torsion of 1.5 or more turns ........................ **Cochlodinium** Schütt

## **HEMIDINIUM** Stein

Text figure R, 4

*Hemidinium* Stein (1888), pp. 91, 97, pl. 2, figs. 23–26.
*Hemidinium,* Eyferth (1879), p. 19.
*Hemidinium,* Saville-Kent (1880–82), pp. 210, 440, 442.
*Hemidinium,* Bergh (1882), p. 694; (1884), pp. 385, 387.
*Hemidinium,* Bütschli (1885), pp. 1008, 1016, pl. 51, fig. 3.
*Hemidinium,* Delage and Hèrouard (1896), p. 384, fig. 667.
*Hemidinium,* Schütt (1896), p. 4, fig. 3.
*Hemidinium,* Mez (1898), p. 217, pl. 6, fig. 286.
*Hemidinium,* Schilling (1891*a*), pp. 274, 275, pl. 8, figs. 23–25, pl. 10, fig. 8.
*Hemidinium,* Lemmermann (1900), p. 115; (1901), p. 358; (1902), p. 260; (1910), pp. 580, 617, 618, figs. 14–18.
*Hemidinium,* Schönichen and Kalberlah (1900), p. 230, pl. 8, fig. 1; (1909), p. 251, pl. 8, fig. 1.
*Hemidinium,* Willey anl Hickson (1901), p. 184, fig. 10.
*Hemidinium,* Paulsen (1908), pp. 94, 95, fig. 127.
*Hemidinium,* Conn (1905), p. 39.
*Hemidinium,* Cavers (1913), p. 183, fig. 9.

DIAGNOSIS.—Gymnodiniidae with incomplete girdle of 0.5 turn; 2 species, from fresh water.

DESCRIPTION.—The body is asymmetrically ellipsoidal to ellipsoidal in form; girdle median to premedian, incomplete, forming less than 0.5 turn of a descending left spiral; sulcus confined to the hypocone. The nucleus is ellipsoidal to spheroidal with chromatin granules. The chromatophores are yellowish to brownish. No stigma. Small species, 24–33$\mu$ long. Fresh water, Europe. Two species.

HISTORICAL DISCUSSION.—This genus was described by Stein (1883) and included but a single species, *H. nasutum* Stein, the type species of the genus. It has no other characteristics of a primitive nature except holophytic nutrition. Levander later (1900*a*) added a second species to the genus, *H. ochraceum*, also from fresh water.

COMPARISONS.—This genus has been generally accepted and widely used as a primitive representative of the Dinoflagellata because of its partially developed girdle. In view of the fact that it is a fresh-water genus, without, as yet, any representative on the sea, it may be that the imperfect condition of the girdle is really a degenerate rather than a primitive one. It has a descending spiral, though incomplete, girdle, and in this particular is nearer *Gyrodinium* than to *Gymnodinium*. Klebs (1883) states that *Hemidinium* has a cell membrane which swells in sulphuric acid and stains yellow in iodine, is finely granular and sometimes striate. It appears, however, to be no more than the pellicle of the unarmored dinoflagellates. The matter should be more fully investigated. The genus is tentatively included in the Gymnodiniidae.

### KEY TO THE SPECIES OF **Hemidinium**

Epicone and hypocone subequal, proximal end of girdle deflected posteriorly........**nasutum** Stein

Epicone much smaller than the hypocone, proximal end of girdle deflected anteriorly ................ ........................................**ochraceum** Levander

### **Hemidinium nasutum** Stein

Text figure R, 4

*Hemidinium nasutum* Stein (1883), pp. 91, 97, pl. 2, figs. 23–26.
*H. nasutum,* Eyferth (1879), p. 19.
*H. nasutum,* Saville-Kent (1880–82), p. 442.
*H. nasutum,* Klebs (1883), pp. 348, 351, pl. 2, fig. 27; (1884), p. 739.
*H. nasutum,* Daday (1884), p. 10.
*H. nasutum,* Bütschli (1885*a*), p. 559, fig. 1; (1885*b*), 1008, 1016, pl. 51, fig. 3.
*H. nasutum,* Dalla Torre (1885), p. 272.
*H. nasutum,* Schilling (1891*a*), pp. 243, 248, 274, 275, pl. 8, figs. 23–25, pl. 10, fig. 8.
*H. nasutum,* Francé (1893), p. 139.
*H. nasutum,* Levander (1894), p. 43; (1900*a*), pp. 58, 64; (1901), p. 6.
*H. nasutum,* Delage and Hèrouard (1896), p. 384, fig. 667.
*H. nasutum,* Entz (1896), p. 22; (1897), pp. xxxi, 52; (1902), p. 126; (1904), pp. 8, 11.
*H. nasutum,* Schütt (1896), p. 4, fig. 3.
*H. nasutum,* Butschinsky (1897), p. 195.
*H. nasutum,* Ludwig (1898), p. 298.
*H. nasutum,* Mez (1898), p. 217, pl. 6, fig. 286.
*H. nasutum,* Schönichen and Kalberlah (1900), p. 230, pl. 8, fig. 1; (1909), p. 251, pl. 8, fig. 1.
*H. nasutum,* Lemmermann (1900), p. 115; (1901), p. 358; (1902), p. 260; (1906), p. 419; (1910), pp. 617, 618, 580, figs. 14–18.
*H. nasutum,* Zacharias (1903), pp. 237, 244.
*H. nasutum,* Paulsen (1908), p. 94, fig. 127.
*H. nasutum,* Kleiber (1911), p. 14.
*H. nasutum,* Senn (1911), p. 64, fig. 6.
*H. nasutum,* Cavers (1913), p. 182, fig. 9.
*H. nasutum,* West (1916), p. 75.

DIAGNOSIS.—Body asymmetrically ellipsoidal, flattened on three sides, rotund on the left; its length 1.75 transdiameters; girdle a descending left spiral of 0.5 turn, its anterior lip protuberant; sulcus reaching postmargin; chromatophores yellow to brown. Length, 24–28μ. Fresh-water ponds and pools in clear water. Europe.

DESCRIPTION.—The body is noticeably asymmetrically ellipsoidal with flattened ventral, right, and dorsal faces, but rotund left face interrupted by the protuberant anterior lip of the girdle. Its length is 1.5 to 1.65 transdiameters at the widest part, which is at the base of the epicone. The epicone and hypocone are subequal, both with asymmetrical, subhemispheroidal apices, the antapex sometimes exhibiting a shallow sulcal notch.

The girdle is incomplete, making 0.5 turn of an evenly descending left spiral with a total displacement of 0.33 of the length of the body. Its anterior lip on the left margin is strongly protuberant, hence the specific name. The posterior lip is more rounded than the anterior. It fades out distally at the middorsal line. The sulcus is confined to the hypocone and extends as a straight furrow from the girdle to the postmargin in which it may form a shallow notch. The two flagella originate near the junction of girdle and sulcus in close proximity.

The nucleus is a small ellipsoid in the left posterior part of the hypocone. Its axes are 0.30 and 0.25 transdiameter in length respectively. Its membrane appears to be double-contoured, and typical chromatin threads have not, as yet, been figured in it.

The peripheral cytoplasm is filled with elliptical reddish brown chromatophores and reddish brown oil drops as stated by Schilling (1913) to be present in the spherical cyst. Klebs (1883) states that this species has a distinct, separable cell wall which swells in soda and sulphuric acid, stains yellow in iodine and brown in chloride of zinc. Schilling (1913) states that it is composed of cellulose, though Klebs had distinctly noted that it does not stain blue on test for cellulose. Further investigation is needed to determine the presence of this so-called cell wall and to determine its nature as compared with the pellicle of the Gymnodinioidae with which we here include it.

DIMENSIONS.—Length, 24–28μ; transdiameter, 16–17μ; nucleus, 7–8μ; cyst, 20μ.

OCCURRENCE.—Originally described by Stein (1883) from Prague, Austria, and later reported by Klebs (1883), Schilling (1891, 1913), Levander (1894, 1900*a*, 1901), Francé (1893), and Dalle Torre (1885), from continental fresh waters in Europe from the Tyrol to Finland. Schilling (1913) states that it is rather common in shaded fresh-water pools, ponds, ditches and swamps in clear water. Butschinsky (1897) reports it as rare in a salt lake near Odessa, Russia, with a concentration of 5 per cent. Since he also reports *Oxyrrhis marinum* (as *Glyphidium marinum*) from the same water, it seems improbable that he has confused the two species. There is no other record of the species from salt or brackish water. Its occurrence therein requires verification. It has not been reported from the Americas.

COMPARISONS.—It appears to be quite distinct from *H. ochraceum* of Levander (1900*a*), who found them both in temporary rain-water pools on rocks in Finland. Both have the thin pellicle, but differ in the position of the girdle, which in this species is more nearly equatorial, as in *Gymnodinium*, while in *G. ochraceum* it is anterior, as in *Amphidinium*.

### **Hemidinium ochraceum** Levander

*Hemidinium ochraceus* Levander (1900*a*), pp. 58, 61, 103, 104, fig. 2.
*H. ochraceum,* Lemmermann (1909), pp. 580, 618, figs. 14, 15.

Diagnosis.—Body broadly ellipsoidal, its length 1.3 transdiameters; epicone about 0.25 of the hypocone; girdle with 0.5 circuit, steeply descending on dorsal face, sulcus not reaching postmargin; yellowish green to reddish brown; length, 23–33μ. Fresh-water pools, Finland.

Description.—This is asymmetrically and broadly ellipsoidal, widest at the middle, its length 1.3 transdiameters, slightly flattened dorsoventrally. The epicone, measured at the proximal end of the girdle, is 0.25 of the total length. It is not separable from the hypocone on the right side. The apex is flattened hemispherical in shape. The hypocone is three times as long as the epicone, elongate hemispheroidal in shape with no sulcal notch in the postmargin.

The girdle is incomplete, making a trifle less than 0.5 turn. From the proximal end it ascends at an angle of 20° above the transverse plane to the left margin, where it turns abruptly posteriorly at an angle of 70° below the transverse plane, terminating in a narrow trough to the right of the middorsal line a little below the equator. It has a net displacement of 0.35 and a total displacement of 0.50 length of the body. The anterior lip is less protuberant than in *H. nasutum,* and the posterior one is broadly rounded. The sulcus proceeds posteriorly from its junction with the girdle about half way to the postmargin. Levander's (1900*a*) interpretation of the girdle and sulcus as a single furrow misconstrues the sulcus. The two flagella arise near each other at the junction of girdle and sulcus. Lemmermann's (1909) copy of Levander's figure is in error in uniting the two flagella at their bases.

The nucleus is spheroidal, 0.33 transdiameter wide, and filled with chromatin grains. It is located in the posterior part of the hypocone. The color is reddish brown anteriorly and yellowish green elsewhere. Chromatophores not designated but presumably present. Cysts yellowish green with reddish brown center, spheroidal.

Dimensions.—Length, 26–33μ; transdiameter, 23–26μ. Cysts, 31μ.

Occurrence.—Described by Levander (1900*a*) as abundant in shallow rainwater pools on rocks on the Skaren Islands, Finland, in association with *H. nasutum* Stein.

Comparisons.—Levander (1900*a*) notes the presence on this species of a thin "shell." If this is not merely a heavy pellicle, but a shell of the type found in *Glenodinium,* this species, perhaps with *H. nasutum,* should be transferred to the thecate Peridinioidae. In any event, this species affords, in this structural particular, an intermediate condition which tends to bridge over the gap between the athecate Gymnodinioidae and the thecate Peridinioidae.

## **AMPHIDINIUM** Claparède and Lachmann

Text figure U

*Amphidinium* Claparède and Lachmann (1858–61), p. 410, pl. 20, figs. 9–12.
*Amphidinium,* Saville-Kent (1880–82), p. 461, pl. 25, figs. 44–46.
*Amphidinium,* Bergh (1882), pp. 693–695.
*Amphidinium,* Bütschli (1885), p. 1011, pl. 54, figs. 6, 7.
*Amphidinium,* Schütt (1896), p. 4, fig. 4.

*Amphidinium,* Delage and Hèrouard (1896), p. 386, fig. 678.
*Amphidinium,* Schönichen and Kalberlah (1900), p. 230, pl. 8, fig. 2; (1909), p. 251, pl. 8, fig. 2.
*Amphidinium,* Calkins (1902), p. 432, fig. 27.
*Amphidinium,* Paulsen (1908), p. 95.
*Amphidinium,* Lohmann (1909), p. 223, figs. 19–21, 26.
*Amphidinium,* Lemmermann (1910), pp. 580, 615, figs. 1–8.
*Amphidinium,* Schilling (1913), p. 13, fig. 9.

Diagnosis.—Body usually compressed; girdle placed far anteriorly, with little or no displacement; sulcus extending from girdle, rarely from apex, to antapex without torsion; epicone relatively minute. Nucleus generally posteriorly or centrally located. Pusules opening anteriorly into the anterior flagellar pore, posteriorly into the posterior pore, or both may be fused into one. No nematocysts present. Plasma colorless with or without chromatophores or colored without chromatophores. Surface may show fine striae, furrows, or ridges may be smooth. Encystment in thin-walled membrane frequent. Nutrition holophytic or holozoic. Length, 12 to 110$\mu$. Marine, fresh and brackish waters. eupelagic and neritic forms; warm or cold temperate seas; 22 species described.

## Organology

The genus *Amphidinium* is, in many respects, the most simply organized of the Gymnodiniidae, yet it anticipates the conditions found in the more highly evolved groups even of the Dinophysidae. The body is without torsion and differs from *Gymnodinium* mainly in the position of the girdle, the greater frequency of a dorsoventral compression of the body and the more frequent possession of chromatophores.

The girdle is placed far anteriorly, at least on the dorsal side, and either forms a circle transversely around the body or turns posteriorly on the ventral side. One species only, *A. scissum* (fig. U, 1), has a displacement of the girdle similar to that found in *Gymnodinium* and *Gyrodinium*. In the other species the ends of the girdle meet without displacement, the apparent exception being *A. sulcatum* (fig. U, 10). In this species the girdle becomes contracted on the right side, while the left side is expanded, forming an apparent displacement of the proximal borders but not of the distal borders of the girdle (fig. U, 26).

The anterior position of the girdle makes the relative sizes of the epicone and hypocone one of the most striking features of the genus. The divergent form, *A. asymmetricum* (fig. U, 5), shows the greatest deviation from the type in this respect, and foreshadows the conditions in *Gymnodinium*. The position of the girdle dorsad, however, is farther anterior than is the case in any species of that genus.

The larger group of species (subgenus *Amphidinium sensu strictu*) shows a strong dorsoventral compression of the body with one exception, *A. sulcatum*,

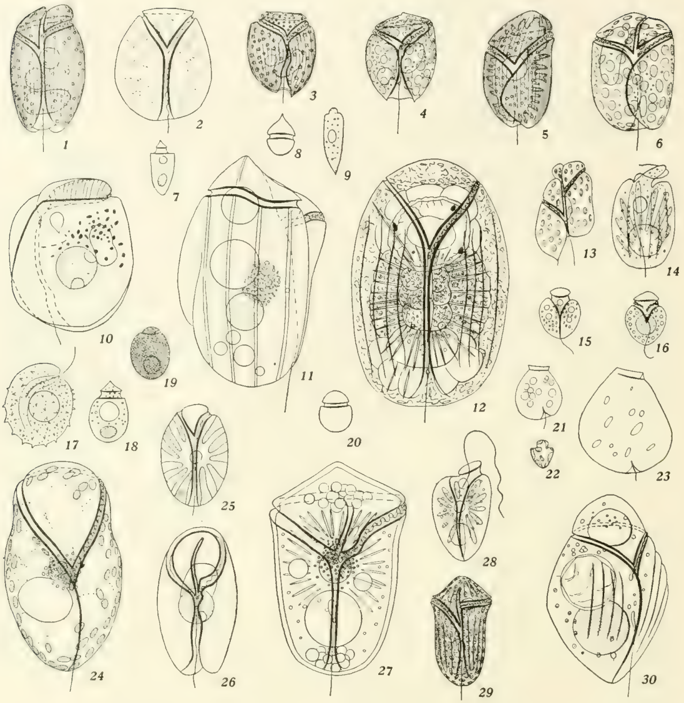


Fig. U. *Amphidinium*. 1. *A. scissum* sp. nov. 2. *A. herdmani* nom. sp. nov. After Herdmann (1911, pl. 8, fig. 5). 3. *A. truncatum* sp. nov. 4. *A. dentatum* sp. nov. 5. *A. asymmetricum* sp. nov. 6. *A. corpulentum* sp. nov. 7. *A. longum* Lohm. After Lohmann (1908, pl. 17, fig. 15). *A. aculeatum* Schr. After Schröder (1911, fig. 1). 9. *A. lanceolatum* Schr. After Schröder (1911, p. 650, fig. 15). 10. *A. sulcatum* Kofoid. After Kofoid (1907, pl. 22, fig. 1). Lateral view. 11. *A. fastigium* sp. nov. Lateral view. 12. *A. cucurbita* sp. nov. 13. *A. corpulentum* sp. nov. × 600. Conjugation? 14. *A. klebsi* nom. sp. nov. After Klebs (1884, pl. 10, fig. 12). 15. *A. lacustre* Stein. After Stein (1883, pl. 17, fig. 21). 16. *A. turbo* sp. nov. 17. *A. aculeatum* Daday. After Daday (1888, pl. 3, fig. 10). 18. *A. crassum* Lohm. After Lohmann (1908, pl. 17, fig. 15). 19. *A. ovoideum* Lemm. After Lemmermann (1896, fig. 1). 20. *A. globosum* Schr. After Schröder (1911, fig. 16). 21. *A. emarginatum* (Clap. and Lach.) Diesing. After Claparède and Lachmann (1853, pl. 20, fig. 11). 22. *A. rotundatum* Lohm. After Lohmann (1908, pl. 17, fig. 9). 23. *A. discoidalis* (Clap. and Lach.). After Claparède and Lachmann (1858, pl. 20, fig. 12). 24. *A. pacificum* sp. nov. 25. *A. operculatum* Clap. and Lach. After Calkins (1902, fig. 27). 26. *A. sulcatum* Kofoid. After Kofoid (1907*a*, pl. 22, fig. 2). 27. *A. vasculum* sp. nov. 28. *A. steini* (Stein) Lemm. After Stein (1883, pl. 17, fig. 9). 29. *A. galbanum* sp. nov. 30. *A. cucurbitella* sp. nov. × 500, except where otherwise stated.

which is strongly compressed laterally (fig. U, 10, 26). This is a condition rare in *Gymnodinium*, being met with there mainly in a few fresh-water forms. Correlated with this form of body is the presence of definite chromatophores. These are lacking in one species only, *A. scissum,* in which the green color is diffused through the cytoplasm. The chromatophores show three distinct types, which may possibly be only phases related to different stages of metabolism or of the life history. The most common form of chromatophore is that found in *A. corpulentum, A. dentatum, A. ovoideum,* and *A. truncatum* (figs. U, 6, 4, 19, 3). These structures are disklike bodies located in the peripheral layer of the cytoplasm, and more or less irregular in shape. They are green in *A. dentatum* and *A. truncatum*, yellow ochre in *A. corpulentum*, and brownish in *A. ovoideum*. Another phase of these extremely labile organelles may be seen in the smaller green bodies in the peripheral zone of *A. scissum*, which may be the remains of larger green chromatophores from which the color has become diffused through the cytoplasm (pl. 2, fig. 22).

Another example of the same type is found in the subgenus *Rotundinium* in *A. pacificum* (pl. 2, fig. 13), in which the chromatophores are pyrite yellow.

The second type of chromatophores is shown in *A. operculatum,* with its long, bandlike chromatophores radiating from a common center near the middle of the body (fig. U, 25). These are also found in *A. herdmani* and *A. steini* (figs. U, 2, 28). A slightly different arrangement obtains in *A. klebsi*, where the chromatophores radiate from a common center located at the posterior end of the body (fig. U, 14). These are brownish (yellow ochre?) in *A. herdmani, A. steini,* and *A. klebsi* (?).

The third type of chromatophore is found in the subgenus *Rotundinium* in *A. asymmetricum* (pl. 1, fig. 1). The single yellow ochre chromatophore is large, filling almost the entire body, with ramifying, pseudopodia-like projections.

In the subgenus *Rotundinium* the body has a robust habit, circular or nearly so in cross-section. With this is correlated, in the larger species, an increasing complexity of cytoplasmic structure, culminating in *A. cucurbita* (pl. 1, fig. 9). This species resembles, in the structural details of its cytoplasm, the subgenus *Pachydinium* in *Gymnodinium* (pl. 3). With four exceptions this group shows a relative absence of chromatophores, the exceptions being *A. rotundatum* (fig. U, 22), with its peripheral, leaflike yellow chromatophores, *A. asymmetricum* (fig. U, 5), with single, large, yellow ochre chromatophore, *A. lacustre* (fig. U, 15), with peripheral, circular, brown chromatophores, *A. galbanum* (fig. U, 29), with peripheral, leaflike chromatophores, and *A. pacificum* (fig. U, 24), with pyrite yellow chromatophores near the surface.

In *A. cucurbita, A. cucurbitella, A. fastigium,* and *A. vasculum* the color is diffused throughout the cytoplasm, while *A. turbo*, *A. longum*, and *A. crassum* are colorless.

The sulcus exhibits various degrees of development in *Amphidinium.* In *A. turbo* (fig. U, 16) it is a very short, V-shaped indentation of the anterior

border of the hypocone. In *A. lacustre* (fig. U, 15) the V-shape trough extends as a narrow line to the antapex. In four species only does it invade the epicone. In *A. corpulentum, A. vasculum, A. scissum,* and *A. sulcatum* (figs. U, 6, 27, 1, 26) it reaches near to and, in the last species, slightly beyond the apex. Its borders posterior to the girdle are frequently extended in flaplike projections. These are exaggerated on the left side in *A. asymmetricum* (fig. U, 5). In *A. sulcatum* (figs. U, 10, 26) the right border is enlarged anteriorly, the left border posteriorly. The antapex may be excavated by the sulcal notch, as in *A. sulcatum* and *A. asymmetricum* or smoothly rounded as in *A. operculatum* (figs. U, 26, 5, 25).

*Amphidinium* possesses the type of pusule found throughout the Gymnodiniidae. One or two may be present, either opening anteriorly into the anterior flagellar pore or posteriorly into the posterior pore. In *A. truncatum* these are merged into one large, irregularly shaped pusule opening into both pores.

The nucleus of *Amphidinium* usually has distinct, moniliform chromatin threads and is without a perinuclear membrane. It is generally found near the center or in the posterior part of the body.

The genus *Amphidinium* shows a narrow range of coloring. The predominant color is green, varying to greenish yellow, and yellow shading to orange in *A. cucurbita* (pl. 1, fig. 9), and to yellow ochre in the other species. It is probable that the brownish color given for many of the earlier described forms is yellow ochre, a common color throughout the Dinoflagellata.

Striae or other surface markings are not so common in *Amphidinium* as in *Gymnodinium* and *Gyrodinium.* Three species, *A. asymmetricum, A. dentatum,* and *A. scissum* (fig. U, 5, 4, 1), show the fine surface striae common to the latter genera. The surface in *A. cucurbitella* (fig. U, 30) and *A. cucurbita* (fig. W, 3) is marked by deep furrows with very fine striations between, quite unlike anything found elsewhere. In *A. fastigium* (fig. U, 11) it is marked by a few distinct ridges and in *A. galbanum* (fig. U, 29) by furrows. The surface markings of *A. klebsi* are too indefinite in Kleb's figure (1885) to be classified.

Nutrition in the species of this genus is both holophytic and holozoic. When chromatophores are present it is presumably holophytic, yet not invariably so. In *A. steini* chromatophores are usually present, yet undoubted evidence of the ingestion of foreign bodies is also given by Stein (1883, pl. 17, figs. 14–16). The chromatophores in these figures are very small. Among our species, *A. scissum* possesses what may be the remains of small chromatophores and also shows the presence of two large food masses. The other forms without chromatophores in most cases show the presence of food bodies within the cytoplasm.

Cyst formation is common throughout the group. Binary fission may take place within a cyst or in the freely swimming forms.

Distribution.—Species of *Amphidinium* have been described mainly from the warm and cool temperate waters. None have been found thus far in tropical seas and only one from the colder northern waters, Mielck (1914) reporting

the presence of *A. rotundatum* in the White and Barents seas. A number of species have been recorded from the Baltic Sea and off the coast of Norway and Sweden. Of these Lohmann (1908) found *A. longum, A. crassum,* and *A. rotundatum* at Kiel, Germany; Lemmermann (1896*b*) described *A. ovoideum* in brackish waters near Plön, Germany; and Stein (1883) figures *A. steini* from Wismar, Germany. *A. operculatum* has been recorded by Claparède and Lachmann (1858–61) from the southwest coast of Norway, by Cleve (1884) from the west coast of Sweden, and by Calkins (1902) from the Atlantic at Woods Hole, Mass.

The only species recorded from the Mediterranean are *A. klebsi* by Klebs (1884) from the Bay of Naples and *A. lanceolatum* by Schröder (1911) from the Adriatic. The only species thus far reported from the Pacific is *A. sulcatum* by Kofoid (1907*a*) off San Diego.

To this single record for the Pacific we add in this paper from the plankton and sandy beach off La Jolla, California, the following twelve new species: *A. asymmetricum, A. corpulentum, A. cucurbitella, A. cucurbita, A. dentatum, A. fastigium, A. pacificum, A. galbanum, A. scissum, A. truncatum, A. turbo,* and *A. vasculum.*

A single species, *A. lacustre,* has been described from fresh-water pools near Prague, Austria, by Stein (1883). Schilling (1913) records the finding of this species in brackish waters in Hungary by Daday.

*Amphidinium* is chiefly a littoral or shore form, but a few species have been described from deeper waters. Six of these are from the Pacific and are the largest species in the genus. *A. cucurbita* and *A. cucurbitella* were found only at 1.5 to 6 miles offshore, from a depth of 80 meters, and *A. sulcatum* in a haul from 165 meters 10.5 miles offshore. *A. operculatum* has been recorded both from deep waters and from a sandy beach, the latter observation made by Spengel at Norderney, Denmark, and recorded by Bergh (1882). Herdman (1911, 1912) found *A. herdmani* with several unknown species of *Amphidinium* in vast quantities on the sandy beach at Port Erin, Isle of Man. The species found on the sandy beach at La Jolla, on the Pacific coast, are *A. scissum, A. asymmetricum, A. corpulentum, A. dentatum,* and *A. truncatum.*

The seasonal record of the appearance of the species of this genus is only fragmentary. Many of them are present throughout the year. Calkins (1902) found *A. operculatum* common at Woods Hole, Mass., from July to September; Bergh (1882) records its presence in enormous masses on the beach at Norderney, Denmark, in December and January. Lohmann (1908) found *A. rotundatum* and *A. crassum* present in the Baltic Sea at Kiel throughout the year. The latter species Lebour (1917*a*) found from June to September at Plymouth Sound, England, and *A. rotundatum* was recorded from the White and Barents seas in June and July by Mielck (1914). *A. klebsi* was recorded by Klebs (1884) from the Bay of Naples in the early spring months. *A. herdmani* was found in vast numbers at Port Erin, Isle of Man, from April to November by Herdman (1911–13).

The species found by us on the Pacific coast were taken in July and August. Plankton hauls have been made throughout the year, but preservative has been immediately added to these hauls, and it is very rarely indeed that these soft, naked forms preserve their identity after contact with the fixing fluid.

## Historical Discussion

The genus *Amphidinium* was established by Claparède and Lachmann (1858–61), who figured *A. operculatum* and two other forms which they thought might be varieties of the same species. These were later established by Diesing (1866) as *A. operculatum* var. *discoidalis* and *A. operculatum* var. *emarginata*. Their allocation, however, in this genus is doubtful, at least until they have been found again. Stein (1883) figured as *A. operculatum* a form which Lemmermann (1900) changed to var. *steini*. Klebs (1884) also figured as *A. operculatum* what we have designated as *A. klebsi*, nom. sp. nov. Using the same species name, Herdman (1911–13) figures still another form which seems to be specifically different from the three previously described under that name. This we have designated *A. herdmani* nom. sp. nov.

In 1888 Daday added to the genus *A. aculeatum* as a new species, a form which has no apparent *Amphidinium* characteristics, if indeed it belongs in the Dinoflagellata at all, which seems doubtful. Schröder (1911) uses the same species name for a totally different form and one which also presents no *Amphidinium* characteristics. These two forms we exclude from the genus. Schröder, in the same monograph, adds *A. globosum* and *A. lanceolatum*. The first of these is without *Amphidinium* characters and must likewise be excluded from the genus. *A. lanceolatum* we regard as an *Amphidinium*, but one which needs to be redescribed.

Stein (1883) described the only fresh-water form in the genus, *A. lacustre*.

Lemmermann (1900) added to the genus as *A. ovoideum* a form previously described by himself (1896) as *Prorocentrum micans*. Lohmann (1908) added the incompletely described species *A. crassum*, *A. longum*, and *A. rotundatum*. *A. sulcatum* was added by Kofoid (1907).

To the eight previously described species, to wit, *A. crassum* Lohmann, *A. lacustre* Stein, *A. longum* Lohmann, *A. operculatum* Claparède and Lachmann emend., *A. ovoideum* Lemmermann, *A. rotundatum* Lohmann, *A. steini* (Stein), and *A. sulcatum* Kofoid, we add twelve new species from the plankton and beach of the Pacific off La Jolla, California, as follows: *A. asymmetricum*, *A. corpulentum*, *A. cucurbitella*, *A. cucurbita*, *A. dentatum*, *A. fastigium*, *A. galbanum*, *A. pacificum*, *A. scissum*, *A. truncatum*, *A. turbo*, and *A. vasculum*, and two more from the literature, *A. herdmani* nom. sp. nov. and *A. klebsi* nom. sp. nov., based on Herdman's (1911–1913) and Klebs's (1884) figures of *A. operculatum*, respectively.

## Subgenera of **Amphidinium**

### Subgenus 1. **Amphidinium** subgen. nov.

Body compressed either dorsoventrally or laterally. Type species *A. operculatum* Claparède and Lachmann. This subgenus includes besides the type, *A. corpulentum* sp. nov., *A. dentatum* sp. nov., *A. herdmani* nom. sp nov., *A. klebsi* nom. sp. nov., *A. ovoideum* Lemm., *A. scissum* sp. nov., *A. steini* (Stein), *A. sulcatum* Kofoid, and *A. truncatum* sp. nov.

### Subgenus 2. **Rotundinium** subgen. nov.

Body not compressed, its dorsoventral and transdiameters being subequal. Type species *A. cucurbita* sp. nov. This subgenus contains in addition to the type the following species: *A. asymmetricum* sp. nov., *A. cucurbitella* sp. nov., *A. fastigium* sp. nov., *A. galbanum* sp. nov., *A. lacustre* Stein, *A. pacificum* sp. nov., *A. turbo* sp. nov., *A. vasculum* sp. nov., and tentatively the following imperfectly described species, *A. crassum* Lohmann, *A. longum* Lohmann, and *A. rotundatum* Lohmann.

## Key to the Species of **Amphidinium**

1. Body compressed either dorsoventrally or laterally (subgenus **Amphidinium**) .................. 2
1. Body circular in cross-section or nearly so (subgenus **Rotundinium**) .................. 11
2. Epicone small, less than 0.5 transdiameter in diameter, body compressed dorsoventrally 3
2. Epicone greater than 0.5 transdiameter in diameter .................. 6
3. Surface without striae .................. 4
3. Surface striate ..................**klebsi** nom. sp. nov.
4. Chromatophores minute, rounded, numerous ..................**ovoideum** Lemm.
4. Chromatophores large .................. 5
5. Chromatophores long, radial ..................**operculatium** Clap. and Lach.
5. Chromatophores irregular ..................**steini** (Stein) Lemm.
6. Body compressed laterally ..................**sulcatum** Kofoid
6. Body compressed dorsoventrally .................. 7
7. Sulcus extending anteriorly to apex .................. 8
7. Sulcus extending only to the girdle .................. 9
8. Chromatophores absent, surface striate ..................**scissum** sp. nov.
8. Chromatophores present, no surface striae ..................**corpulentum** sp. nov.
9. Hypocone striate, minute green chromatophores ..................**truncatum** sp. nov.
9. Hypocone not striate, chromatophores larger .................. 10
10. Chromatophores green, disk-shaped ..................**dentatum** sp. nov.
10. Chromatophores yellow, long, radiating from center ..................**herdmani** nom. sp. nov.
11. Large species, over $75\mu$ in length .................. 12
11. Small species, not over $75\mu$ in length .................. 16

12. Plasma yellow, length over $100\mu$ .......... 13
12. Plasma colorless or greenish yellow, length less than $100\mu$ .......... 14
13. Surface with furrows and fine striae .......... **cucurbita** sp. nov.
13. Surface with few ridges .......... **fastigium** sp. nov.
14. Ectoplasm thick, color yellow .......... **vasculum** sp. nov.
14. Periplast thin .......... 15
15. Surface with longitudinal furrows .......... **cucurbitella** sp. nov.
15. No furrows .......... **pacificum** sp. nov.
16. Length over $30\mu$ .......... 17
16. Length less than $30\mu$ .......... 18
17. Body asymmetrical, one leaflike chromatophore, surface finely striate .......... **asymmetricum** sp. nov.
17. Symmetrical, many elliptical chromatophores, coarsely striate .......... **galbanum** sp. nov.
18. Length less than 1.5 transdiameters .......... 19
18. Length over 1.5 transdiameters .......... 21
19. Hypocone subconical, chromatophores bright yellow .......... **rotundatum** Lohmann
19. Hypocone subspheroidal .......... 20
20. Marine, colorless .......... **turbo** sp. nov.
20. Fresh water, brown chromatophores .......... **lacustre** Stein
21. Body stout, length 1.6 transdiameters .......... **crassum** Lohmann
21. Body elongated, length over 2 transdiameters .......... **longum** Lohmann

## **Amphidinium aculeatum** Daday and **Amphidinium aculeatum** Schröder

Text figures U, 8, 17

*Amphidinium aculeatum* Daday (1888), p. 104, pl. 3, fig. 10.
*A. aculeatum* Schröder (1900), p. 13; (1911), pp. 616, 650, fig. 14, as a new species.
*A. aculeatum*, Lemmermann (1901*a*), p. 358.
*A. aculeatum*, Kofoid (1907), p. 301.
*A. aculeatum*, Herdman (1911*b*), p. 72; (1911*c*), p. 39.

SYNONYMY.—Under this name Daday (1888) figured (our text fig. U, 17) an organism from the Gulf of Naples which has no apparent affinities with the genus *Amphidinium*. It has no girdle and is covered with a "Panzer," or coat of mail, thickly beset with spines. Whatever its affinities may be, they must be looked for outside the genus *Amphidinium*. Schröder (1900) accepts Daday's species, yet in a later memoir (1911) he figures another organism (our text fig. U, 8), from the Adriatic Sea, as "*Amphidinium aculeatum* nov. spec." which is unlike Daday's form and at the same time presents no *Amphidinium* characteristics. Its girdle is slightly posterior to the median plane, making the epicone and hypocone subequal. These characters alone would suffice to throw it outside the genus *Amphidinium*. Too little data are given to place it elsewhere with any degree of certainty.

### **Amphidinium asymmetricum** sp. nov.

Plate 1, figure 1; text figure U, 5

Diagnosis.—Body asymmetrically ellipsoidal, longest on its left side, epicone very asymmetrical; girdle a steep spiral, deflected posteriorly at both ends; sulcus confined to the hypocone; chromatophore yellowish, ramifying; littoral habitat. Length, 48–52$\mu$. Pacific off La Jolla, California, July.

Description.—The body is asymmetrically ellipsoidal, subcircular in cross-section, flattened dorsally, rotund laterally and ventrally, its transverse and dorsoventral diameters about equal throughout the middle third of the body. The epicone is very asymmetrical, its length at its left side only 0.1 and at the right ventral region nearly 0.5 of the total length. The apex is asymmetrically rounded in ventral view and flattened in the dorsal half in lateral view. Its total volume is about 0.2 that of the whole body. The hypocone is sack-shaped, more symmetrical than the epicone, but still shows some elongation in the left dorsal region homologous with that of the longer left horn of *Ceratium* and many other Dinoflagellata. Its greatest length is 1.6 transdiameters and is found mid-dorsally. The antapex is broadly rounded but longest at the left and dorsad to the main axis.

The girdle is a rounded trough, ascending about 5 furrow widths from the flagellar pore to the dorsal region, passing horizontally across this and descending thence in a uniform slope of 30° on the right face, increasing to 40° on the ventral face in its own distalmost part. Its total displacement between the proximal and distal regions is nearly 0.5 transdiameter. The transverse flagellum completely encircles the body. The length of the sulcus is 0.68 of the total length. It turns to the left anteriorly, and becomes a deep fold in the median plane through the hypocone. It does not extend upon the epicone. Its left border forms a flap which overhangs its right side. The longitudinal flagellum extends posteriorly beyond the antapex for 0.7 of the total length. The posterior flagellar pore is hidden in the deep sulcus.

The surface is faintly striate with fine parallel lines equidistant on both epicone and hypocone, and about ten on the radius. The amyloid body is spheroidal, homogeneous in appearance in life, 0.28 transdiameter in diameter, and centrally located. It is surrounded by a halo of sparsely scattered subspheroidal, highly refractive, oil globules and the whole is enclosed in an unusually large and continuous chromatophore with blunt, finger-like, peripheral processes which radiate in all directions to the surface. Its color is a uniform pale yellow ochre. The nucleus was not certainly located. It probably lies posterior to the amyloid body as in *A. operculatum*.

Dimensions.—Total length, 50$\mu$; transverse diameter at widest point, 30$\mu$; dorsoventral diameter, 28$\mu$; diameter of amyloid body, 7.5$\mu$.

Occurrence.—Moderately frequent in washings from beach sand on the ocean beach at La Jolla, California, in July, 1914.

Comparisons.—This species is a divergent type of *Amphidinium*, not far from the *Gyrodinium*-like species of *Gymnodinium* in respect to the large size of the epicone. The striations are similar to those frequently found in *Gyrodinium*. It has been placed in *Amphidinium* because of (1) the asymmetry of the epicone, which is marked and in the same direction as in *A. operculatum;* (2) the deep ventral sulcus and left flap; and (3) the arrangement of the chromatophore with respect to the amyloid body. All these features are so consistently indications of *Amphidinium* that the slightly excessive size of the epicone may be safely disregarded, especially since intermediate stages in size

of epicone are found in *A. truncatum, A. scissum,* and *A. sulcatum* (figs. U, 3, 1, 10). The species is thus a divergent member of the section of the genus having the larger epicone.

### Amphidinium corpulentum sp. nov.

Plate 1, figure 11; text figures U, 6, 13

Diagnosis.—A small species with body stout, elongated rotund, its length 1.55 transdiameters, dorsoventrally compressed to about 0.5 transdiameter; epicone about 0.25 of the total length, girdle anterior, sulcus extending around apex of epicone to antapex with left flap on hypocone, color ochraceous, littoral habitat. Length, 46–54$\mu$. Pacific at La Jolla, California, July.

Description.—The body is stout, sack-shaped, its length 1.5–1.6 transdiameters, flattened dorsoventrally to about 0.5 transdiameter. Epicone 0.20–0.25 of the total length, subconical in outline with slightly convex sides forming an angle of 30° in ventral and 60° in lateral view. Its diameter almost equals that of the epicone. Its height is 0.66 of its base in lateral view and 0.60 of the base in its greatest ventral extension. Its apex is broadly rounded and partially encircled by the terminal loop of the anterior end of the sulcus. The hypocone forms 0.75–0.80 of the total length and has straight sides for 0.75 of its length. The antapex is broadly rounded in a flattened semicircular outline scarcely notched by the distal end of the sulcus.

The girdle curves sharply anteriorly at its proximal end at an angle of 45°, reaching the horizontal at the end of the first quarter of the turn, continues horizontally to its distal quarter, where it turns posteriorly at an angle of 30° without much curvature to its junction with the sulcus. Its displacement posterior to its proximal end is about a furrow's width. The V-shaped junction is thus markedly asymmetrical. The furrow is deeply incised with prominent lips. The anterior flagellar pore opens at the junction of girdle and sulcus. The sulcus extends the full length of the body in an almost rectilinear course from the antapex anteriorly upon the epicone to within less than two furrows' width of the apex, where it makes an abrupt turn to the left and forms a faint semicircle about the left side of the apex. It sinks deeply into the hypocone and its left margin forms an overhanging flap. It flares distally at the antapex in a broad posteroventral excavation. The longitudinal flagellum arises from the posterior flagellar pore at a point about 0.33 of the length of the hypocone posterior to the distal end of the girdle. It projects beyond the body for a distance equal to 0.75 of the total length of the body.

The surface has no evident striations. The nucleus, in the individual shown in the figure, was elongate, narrowly reniform, and was located in the right half of the epicone with its longer axis parallel to the major axis of the body. Its length nearly equals the transdiameter and its diameter was about 0.3 its length. The body was packed, especially in the peripheral regions, with numerous small rounded ochraceous chromatophores which gave to the whole body a diffuse pale yellow ochre tone. Pusules, amyloid body and oil globules were not noted.

Dimensions.—Total length, 46–54$\mu$; greatest transdiameter, 30–34$\mu$; dorsoventral diameter, 17$\mu$; length of nucleus, 26–30$\mu$.

Occurrence.—This species was found throughout July, 1914, in beach sand off La Jolla, California. It was especially abundant during the latter half of the month.

REPRODUCTION.—Among the numerous individuals under observation one pair (text fig. U, 13) was found in what appeared to be a late phase of conjugation. This conjecture is based upon the correctness of Stein's figures (1883, pl. 17, figs. 25–27) of conjugation in *Amphidinium lacustre*. In his figures and in our pair the two individuals are fused together in the regions of the ventral pores and are slightly displaced anteroposteriorly. One pair could not be separated by manipulation and both in life and after fixation in Bouin's fluid and staining in borax carmine was found to contain only a single spheroidal nucleus.

In view of the lack of reliable information regarding fission, and especially concerning the occurrence and manner of sexual reproduction in the Dinoflagellata, it is quite possible, indeed highly probable, that this is only an early stage in approaching binary fission in which the motor organs have divided but the nucleus is still in the prophase. This sequence in the phenomenon of fission is the usual one among some of the Euflagellata (see Kofoid and Swezy, 1915).

COMPARISONS.—The grounds for including this species in the genus *Amphidinium* are at best but slight. The only morphological grounds are (1) the left flap of the sulcus, (2) the dorsoventral compression, and (3) the relatively small size of the epicone. These characters are found in whole or in part in *A. truncatum, A. scissum, A. asymmetricum,* and *A. dentatum* (figs. U, 3, 1, 5, 4).

The relationships thus established appear to be more significant than the form of girdle, which is the one character relating the species to *Gymnodinium*. It is obvious, however, that the inclusion in *Amphidinium* of a species with so large an epicone as that in *A. corpulentum* will necessitate an emendation to the characteristics of the genus as defined by Schütt (1896).

*Amphidinium corpulentum* has a form of sulcus similar to that of *A. scissum* encircling an apical lobe on the epicone, a left ventral flap along the sulcus as in *A. asymmetricum* and dorsoventral compression as in *A. scissum* and *A. truncatum*. It belongs, therefore, in that section of the genus.

## **Amphidinium crassum** Lohmann

Text figure U, 18

*Amphidinium crassum* Lohmann (1908), pp. 252, 261, 262, 366, 368, pl. 17, fig. 16; (1911), pp. 30, 31, fig. 12*g*.
*A. crassum,* Paulsen (1908), p. 96, fig. 130.
*A. crassum,* Herdman (1911*b*), p. 71; (1911*c*), p. 38.
*A. crassum,* Ostenfeld (1913), p. 338.
*A. crassum,* Lebour (1917*a*), table 1; (1917*b*), p. 188, fig. 2.
*A. crassum,* Lemmermann (1910), p. 615.

DIAGNOSIS.—A minute species with ovoidal body, its length 1.50 transdiameters; girdle anterior; epicone minute. Length, 27$\mu$. Baltic Sea off Kiel, Germany, throughout the year.

DESCRIPTION.—Body broadly oval, rounded posteriorly and pointed anteriorly, its length 1.59 transdiameters at the widest part. The epicone is a minute caplike portion having a length of 0.16 of the total length of the body. It is conical in shape (90°) with a sharply pointed apex. The hypocone is rotund ovoidal with broad rounded antapex, widest about its middle, and in length 0.67 of the total length.

Lohmann's (1908, 1911) figures are both apparently dorsal views which show the girdle passing transversely across the body and give no indication of the sulcus. The girdle is wide, 0.17 transdiameter, and rather deeply impressed. Its distance from the apex is about 0.16 of the total length of the body.

The nucleus is a small ellipsoidal body lying near the antapex. Its major and minor axes are about 0.4 and 0.3 transdiameters, respectively. The central part of the cytoplasm is usually occupied by a large, yellow brown body, probably a food body. The remainder of the cytoplasm contains numerous minute spherules.

DIMENSIONS.—Length, 27μ; transdiameter, 17μ; axes of nucleus, 7 and 5μ.

OCCURRENCE.—Figured by Lohmann (1908, 1911), from the Baltic Sea off Kiel, Germany. He records it as being present throughout most of the year. The only other record of its occurrence is that of Lebour (1917*b*) from Plymouth Sound, England.

## **Amphidinium cucurbita** sp. nov.

Plate 1, figure 9; text figures U, 12, W, 3

DIAGNOSIS.—A large species with rotund ellipsoidal body, its length 1.46 transdiameters, girdle far anterior with no displacement; sulcus extends from girdle to antapex; surface with both striae and furrows; color yellow. Length, 110μ. Pacific off La Jolla, California, June to August.

DESCRIPTION.—The body is rotund ellipsoidal, with broad apices, its length 1.46 transdiameters at the widest part. The epicone occupies only a minute portion of the body, its length on the dorsal and lateral sides being about 0.07 of the total length of the body. It extends posteriorly on the ventral side for a length of 0.36 of the total length, forming a triangular portion of about 55°. Its greatest width is 0.56 of the transdiameter of the hypocone. In ventral view it thus forms the sector of a hemisphere. The hypocone has a length on the dorsal and lateral faces of the body of 0.9 of the total length of the body. Its sides are subparallel for the middle third of their length, the posterior third being hemispherical and the anterior sloping to the girdle. Both the apex and antapex are broadly rounded, almost flattened, the latter being sometimes slightly indented by the sulcal notch.

The girdle is placed far anteriorly, its distance from the apex on the dorsal and lateral sides being about 0.07 of the total length of the body. Ventrally both ends of the girdle turn abruptly posteriorly to meet the girdle at a distance of 0.36 of the total length of the body from the apex. The ends are without displacement. The furrow is narrow and deeply imbedded with sharp-angled borders. The sulcus extends from the girdle to the antapex as a deep, narrow trough, the sides of which become widely deflected near the posterior end of the body. Its depth also increases posteriorly, until it has a depth of nearly 0.5 of the dorsoventral diameter of the body. Its sides are smoothly rounded and in front of the posterior pore may overlap sufficiently to obscure the furrow. The anterior flagellar pore opens at the junction of the girdle and sulcus and the posterior pore a short distance from the antapex.

The nucleus is reniform in shape and is located in the posterior portion of the body. Its chromatin structure could not be analyzed. Its major and minor axes are 0.45 and 0.26 transdiameters respectively.

A small club-shaped pusule opens into each flagellar pore. The cytoplasm is coarsely granular, with a great complexity of structure in all the individuals observed. The midventral portion of the body in the region of the pusules is usually filled with numerous small, dark, refractive granules. Most of these have been omitted in the figures for the sake of clearness. Dorsad from these are large vacuoles, and radiating out from them towards the surface of the body are numerous long, slender greenish rodlets interspersed between long, narrow vacuoles. Both the anterior and posterior regions are filled with large vacuoles or food masses. Small oil droplets are scattered through the remaining cytoplasm.

Vacuoles containing fluid of the same pink color as the pusules are usually present. The general color is a deep, rich yellow.

The surface of the body on the hypocone is marked with deep, parallel furrows, about 20 in number in the circuit of the body. These may be arranged in groups of 3, 1, 5, or may be equidistant. They usually die out before reaching the girdle and the antapex. Between the furrows are found fine equidistant, parallel surface lines of dots, usually about eight between furrows.

DIMENSIONS.—Length, 95 to 110μ; transdiameter, 75μ; axes of nucleus, 32 and 23μ.

OCCURRENCE.—The first individual was taken July 12, 1917, 4 miles off La Jolla, California, in a haul from 80 meters to the surface and in a surface temperature of 20°5 C. Three individuals were recorded July 20, in a haul 6 miles offshore from 80 meters to the surface and in a surface temperature of 21° C. Four more were taken July 27, 4 miles offshore at the same depth and at a surface temperature of 21°9 C. The same number was again observed August 21, in a catch taken 5 miles offshore, in a haul from 83 meters to the surface and in a surface temperature of 21°6 C.

COMPARISONS.—This is by far the largest species of *Amphidinium* thus far described. It presents undoubted affinities with that group, however, as shown by the relatively small, operculum-like epicone. Its large size, rotund habit, and presence in the deeper oceanic waters make it a possible connecting link with *Gymnodinium*. It also exhibits cytoplasmic differentiation similar to that found in *G. dogieli* and *G. costatum*, and without parallel elsewhere in the genus *Amphidinium*.

## **Amphidinium cucurbitella** sp. nov.

Plate 1, figure 6; text figure U, 30

DIAGNOSIS.—This is a medium sized species with broad almost biconical body, its length 1.6 transdiameters; girdle anterior, without displacement; sulcus extending from girdle to antapex; surface striate and furrowed; color green, holozoic. Length, 85μ. Pacific off La Jolla, California, July.

DESCRIPTION.—The body is broadly ellipsoidal, approaching biconical (50°), widest in the middle and tapering towards both apices, its length 1.6 transdiameters at the widest part, subcircular in cross-section. The hypocone greatly exceeds the small epicone, its length being greater by 0.53 of its own length. The epicone is small, rounded, caplike, with a longer, pointed ventral portion. It has a length above the anterior flagellar pore on the ventral side of 0.36 and on the dorsal side of 0.2 of the total length of the body. The hypocone has a length on the dorsal side

of about 0.79 of the total length of the body. It is narrowed anteriorly to about 0.66 of its widest transdiameter, which is at the equator of the body midway between the apices. It tapers posteriorly to the rounded antapex, which is narrower and more pointed than the apex.

The girdle is anterior in position, its distance from the apex being 0.2 of the total length of the body on the dorsal and lateral sides. Ventrally both sides of the girdle are deflected posteriorly until they meet the sulcus at about 0.36 of the total length of the body from the apex. The furrow is a narrow, rather shallow depression with smoothly rounded borders. The sulcus is a narrow trough extending from the girdle to the antapex. The anterior flagellar pore is located at the junction of the girdle and sulcus, the posterior pore at a point about 0.6 of the distance between the junction and the antapex.

The nucleus is a relatively small, spherical body found in the posterior portion of the hypocone. It is filled with fine, moniliform chromatin strands. Its axis is about 0.37 transdiameter. Small club-shaped pusules open into each flagellar pore. The cytoplasm is finely granular, densely so in the central portion of the body, with numerous blue green oil droplets scattered through it. In the anterior end of the body a large vacuole is found and behind it a large food mass enclosed in a vacuole. The general color of the organism is a yellow green with a trace of orange in the denser parts. The surface is finely striate with minute blue green rodlets arranged in a linear series, interspersed at every third row with continuous lines, equidistant and longitudinal. In additon the surface of the hypocone is deeply impressed with longitudinal, parallel grooves. These are arranged in groups of four and are relatively short, fading out before reaching the girdle and antapex. None could be detected on the epicone.

Dimensions.—Length, 85$\mu$; transdiameter, 53$\mu$; diameter of nucleus, 20$\mu$.

Location.—This was first seen July 20, 1906, in a surface haul made with a No. 20 net, 1.5 miles off La Jolla, California. Two individuals were taken July 27, 1917, 4 miles off La Jolla, in a haul from 80 meters to the surface and in a surface temperature of 21°9 C.

Comparisons.—This species and *A. cucurbita* are the only ones in the genus which present the peculiar combination of deeply marked furrows and fine striae on the surface. These differ slightly in the two species. The cytoplasmic structure is simpler in this species than in *A. cucurbita*, yet presents the same evidences of holozoic nutrition.

## **Amphidinium dentatum** sp. nov.

Plate 10, figure 111; text figure U, 4

Diagnosis.—A small species with body broad, almost squarish in ventral view, dorsoventrally compressed, its length 1.25 transdiameter; girdle anterior, without displacement; sulcus extending from girdle to hypocone; blue green chromatophores; littoral habitat. Length, 40$\mu$. Pacific at La Jolla, California, August.

Description.—The body has an almost squarish outline in ventral view, dorsoventrally compressed to about 0.5 transdiameter, widest in the middle, its length 1.25 transdiameters at the widest part. The epicone is small, triangular in ventral view with a width of 0.75 transdiameter. It extends posteriorly on the ventral side about 0.3 of the total length of the body, its sides forming an angle of 70°. It is slightly asymmetrical with the left side higher than the right. The apex is a short, toothlike, dextrally flexed projection. The hypocone is broad and rotund

ventrally, with the left side longer and slightly less convex than the right. The antapex is excavated ventrally by the sulcal notch, broad and rounded on the dorsal side, the right and left borders of the sulcus extending posteriorly in slender, toothlike points.

The girdle is somewhat asymmetrical in position, located about 0.1 of the total length of the body below the apex on the dorsal side, with the distance less on the left and slightly greater on the right sides. Ventrad, both ends turn posteriorly and meet at a point distant from the apex about 0.3 of the total length of the body. The furrow is wide, about 0.09 transdiameter, and deeply impressed, with overhanging borders. The sulcus extends from the girdle to the antapex in a slightly sinuous line which flares widely in the distal half of its course, at the same time expanding dorsad, deeply excavating the ventral part of the body. The anterior flagellar pore opens at the junction of the girdle and sulcus, the posterior pore slightly posterior to the midpoint between girdle and antapex.

The nucleus is an ellipsoidal body found on the left side of the sulcus below the girdle. Its major and minor axes are about 0.46 and 0.25 transdiameters in length, respectively. A large sacklike pusule opens into each flagellar pore. These are connected below their openings by a slender canal. The cytoplasm is clear and colorless. In the peripheral layer are numerous, disklike chromatophores of a dull, blue green color and many minute, dark, highly refractive granules. No striae or other surface markings could be detected.

DIMENSIONS.—Length, 40$\mu$; transdiameter, 32$\mu$; axes of nucleus, 15 and 8$\mu$.

OCCURRENCE.—This species was found in the beach sand at La Jolla, California, in August, 1917.

COMPARISONS.—This species has much in common with *A. truncatum* (fig. U, 3). The size and shape of the epicone and the lack of surface striae serve, however, to set it apart from that species.

## **Amphidinium discoidalis** Diesing

Text figure U, 23

*Amphidinium operculatum* Claparède and Lachmann (1858–61), p. 411, pl. 20, fig. 12 only.
*A. operculatum* var. *discoidalis* Diesing (1866), p. 98 (384).

DIAGNOSIS.—A small species with broadly ovoidal body, its length, 1.13 transdiameters; girdle anterior; sulcus (?); colorless. Length, 47$\mu$. North Sea on the coast of Norway.

DESCRIPTION.—The body is broadly ovoidal, widest posteriorly, its length 1.13 transdiameters at the widest part. The epicone is minute, with a length of about 0.05 of the total length of the body. The apex is broad and truncate. The hypocone is very broad posteriorly, narrowing anteriorly, with broad, rounded antapex. A dorsal view only of this form is given by Claparède and Lachmann (1858–61), hence the structure of the ventral surface is unknown. The girdle is far anterior and passes transversely across the dorsal side of the body. Its distance from the apex is about 0.05 of the total length of the body. The cell contents as figured by Claparède and Lachmann consist of a few spherules and rod-shaped bodies, probably oil drops and food masses.

DIMENSIONS.—Length, 47$\mu$; transdiameter, 41$\mu$.

OCCURRENCE.—Figured by Claparède and Lachmann (1858–61) from the North Sea on the coast of Norway.

SYNONYMY.—This was figured by Claparède and Lachmann as a form of *Amphidinium operculatum*, possibly a different species. Diesing (1866) names it *Amphidinium operculatum* var. *discoidalis*. Its final disposition awaits re-examination of Norwegian material. It appears to be near *A. herdmani*.

### **Amphidinium emarginatum** Diesing

Text figure U, 21

*Amphidinium operculatum* var. Claparède and Lachmann (1858–61), p. 411, pl. 20, fig. 11.
*A. operculatum* var. *emarginata* Diesing (1866), p. 98 (384).

DIAGNOSIS.—A minute species, with broadly ovoidal body, its length 1.1 transdiameters; girdle anterior; sulcus (?); colorless. Length, 24µ. North Sea on the coast of Norway.

DESCRIPTION.—The body is broadly ovoidal, widest posteriorly, its length 1.1 transdiameters at the widest part. The dorsal side only is figured by Claparède and Lachmann (1858–61), hence the course of the girdle on the ventral side as well as the sulcus are unknown. The epicone is a minute, caplike portion at the anterior end marked off from the rest of the body by the girdle. It has a length of 0.07 of the total length of the body. The apex is truncate. The hypocone is somewhat spatulate. Its anterior end has a width of 0.36 of the greatest transdiameter of the body. The apex is broad, almost subtruncate.

The girdle passes transversely across the body at the anterior end, its distance from the apex being 0.07 of the total length of the body. A few rounded spherules occupy the middle portions of the body. Nucleus and pusules are not figured.

DIMENSIONS.—Length, 24µ; transdiameter, 21µ.

OCCURRENCE.—Figured by Claparède and Lachmann (1858–61) from the North Sea off the coast of Norway.

SYNONYMY.—This was described by Claparède and Lachmann (1858–61) as *Amphidinium operculatum* variety, possibly a different species. Diesing (1866) describes it as *Amphidinium operculatum* var. *emarginata* (Clap. and Lach.). It is near *A. herdmani*. Its final disposition awaits re-examination of Norwegian material.

### **Amphidinium fastigium** sp. nov.

Plate 2, figure 18; text figure U, 11

DIAGNOSIS.—A large species with irregularly ellipsoidal body, its length 1.61 transdiameters; girdle without displacement; sulcus extending to antapex; color grey green. Length, 102µ. Pacific off La Jolla, California, June, July.

DESCRIPTION.—The body is irregularly ellipsoidal, slightly pointed anteriorly, broadly rounded posteriorly, its length 1.61 transdiameters at the widest part. Its transdiameter and dorso-ventral diameter are subequal. The epicone has the shape of a low, broad cone with the apex more or less flattened and a deep, wide trough extending down the ventral face. Its length on the dorsal and ventral sides is 0.3 and 0.4 of the total length of the body respectively. The

hypocone is an irregular sacklike body with a deep groove on the proximal part of the ventral face and a shallow one on the distal part of the dorsal face. The antapex is broad and rounded.

The girdle lies at a distance from the apex on the dorsal and ventral sides of 0.3 and 0.4 of the total length of the body respectively. The furrow is wide, about 0.06 transdiameter, and is deeply impressed, undercutting the anterior border and smoothly curving out to the posterior one. Both lips are outlined by a double-contoured, blue green line. The exact relations of the sulcus are difficult to distinguish. It seems to invade the epicone at the base of the trough which indents its ventral face. Posteriorly it extends to within a short distance of the antapex. The anterior flagellar pore is found at the junction of girdle and sulcus, and the posterior pore a short distance in front of the antapex.

The nucleus is an ellipsoidal body filled with moniliform chromatin strands. It is slightly posterior to the central part of the organism. Its axis is about 0.36 transdiameter in length.

The cytoplasm is finely granular and rather dense in appearance. In the central part of the body is a mass of dark, refractive granules. Anteriorly is a large body of greyish color, presumably a food mass, and nearer the center a larger, reddish brown body. Posterior to the nucleus are other bodies grey and reddish brown in color. A few small spherules and minute refractive granules are scattered through the remainder of the cytoplasm. The general color of the organism is dull grey green. The surface of the body is marked by a few double-contoured lines or ridges, about five on one face of the hypocone, fewer on the epicone. These extend from the girdle to the apices.

Dimensions.—Length, 102μ; transdiameter, 63μ; axis of nucleus, 23μ.

Occurrence.—This species was first seen in a surface haul made at the end of the pier at the Biological Station at La Jolla, California, June 26, 1917. On July 25 it was taken in a haul 11 miles offshore, from 80 meters to the surface and in a surface temperature of 21°75 C. On July 27 it was noted in a haul taken 4 miles offshore, from 80 meters to the surface and in a surface temperature of 21°9 C.

Comparisons.—This is an aberrant species, *Amphidinium*-like in the relation of epicone and hypocone, yet possessing characters which clearly mark it off from the other species of that genus. In one individual noted, a stout, laterally projecting tentacle was thrust out from the distal part of the sulcal area. This greatly resembled the prod of *Erythropsis*. The individual possessing it was not active, so that nothing can be said as to its motility or normality. It was possibly only a temporary protoplasmic process.

## **Amphidinium galbanum** sp. nov.

Plate 1, figure 4; text figure U, 29

Diagnosis.—A small species with subcylindrical body, its length, 1.92 transdiameters; girdle anterior, displaced 0.44 transdiameter, sulcus extending from near apex to antapex; surface furrowed; bright green yellow chromatophores. Length, 48μ. Pacific off La Jolla, California, July.

Description.—The body is small, subcylindrical with the anterior end forming a conical cap, the posterior end rounded, slightly wider anteriorly, its length 1.92 transdiameters at the widest part. The hypocone greatly exceeds the epicone in size, its length being greater by 0.63. The

epicone has the shape of a broad, flat cone of about 105° with blunt apex. Its length is about 0.22 of the total length of the body, except for a slender point extending posteriorly on the right side of the sulcus with a length of 0.45 of the total length. The hypocone is long, with a length of 0.73 of the total length of the body. Its sides are subparallel for about 0.7 of their extent, flaring slightly around the girdle and rounded posteriorly to the broad, symmetrical antapex.

The girdle encircles the body near the anterior end. Its proximal end joins the sulcus at a distance from the apex of 0.22 of the total length of the body. It passes around the body transversely for about 0.8 of a turn, when it is abruptly deflected posteriorly, with a displacement of 0.44 transdiameter, meeting the sulcus at an angle of about 45°. The furrow is about 0.12 transdiameter in width, and deeply impressed. The sulcus begins a short distance from the apex and extends posteriorly to the antapex in a slightly sinuous course. The trough is shallow anteriorly, deepening posteriorly with a wide flare of the borders in the antapical region. The anterior flagellar pore is found at the proximal junction of the girdle and sulcus, the posterior pore about midway between the distal junction and the antapex.

The nucleus is a relatively large, spheroidal body in the posterior half of the hypocone. It is filled with fine beaded chromatin strands. Its axis is 0.52 transdiameter.

A small sacklike pusule opens into each flagellar pore. The cytoplasm is granular and alveolar in structure, with relatively coarse alveoli. This is omitted in the figures for the sake of clearness. The color of the cytoplasm is pearl grey. In the peripheral layer are numerous blue green oil droplets and leaflike, bright green yellow chromatophores. These are placed closely together through the entire peripheral layer of the cytoplasm. The surface of the body is marked by longitudinal grooves, about twelve in number, across one face. On the epicone these are radially arranged around the apex and die out before reaching the girdle. On the hypocone they are subparallel, fading out before reaching the girdle and the antapex.

DIMENSIONS.—Length, 48–67$\mu$; transdiameter, 25–32$\mu$; diameter of nucleus, 14$\mu$.

OCCURRENCE.—The first individual was taken July 20, with a No. 25 silk net, 6 miles off La Jolla, California, in a haul from 80 meters to the surface and in a surface temperature of 21° C. A second one was taken July 24, 2.75 miles off La Jolla, in a haul 80 meters to the surface and in a surface temperature of 21°9 C.

COMPARISONS.—Like *A. cucurbita* this species stands near the border line dividing *Amphidinium* from *Gymnodinium*. The relatively minute size of the epicone places it with the former genus rather than with the latter.

### **Amphidinium globosum** Schröder

Text figure U, 20

*Amphidinium globosum* Schröder (1911), pp. 616, 651, fig. 16.
*A. globosum,* Schiller (1912), p. 493.

SYNONYMY.—This form was figured by Schröder (1911) from the Adriatic Sea near Rovigno, Austria. It is almost globular in form with minute brown chromatophores, the length of the hypocone being only twice that of the epicone. The relation of epicone and hypocone is not the characteristic one of the genus *Amphidinium*, and is sufficient to make its inclusion with that genus doubtful. The data given are too slight to place it with any degree of certainty, at least until its characteristics have been more fully analyzed.

## **Amphidinium herdmani** nom. sp. nov.

Text figure U, 2

*Amphidinium operculatum,* Herdman (1911*a*), p. 554; (1911*b*), pp. 71–75, pl. 8; (1911*c*), pp. 38–47, figs. 23–26; (1912), pp. 28–36, figs. 8–11; (1913), pp. 19–23, fig. 6.

DIAGNOSIS.—A small species with broadly ellipsoidal body in ventral view, dorsoventrally compressed, its length 1.16 transdiameters; girdle anterior; sulcus extending from girdle to antapex; color bright yellow. Length, 50$\mu$. Irish Sea, beach sand at Port Erin, Isle of Man, April to November.

DESCRIPTION.—The body is broadly ellipsoidal in ventral view, dorsoventrally flattened, rounded posteriorly and truncate anteriorly, its length 1.16 transdiameters at the widest part. The epicone is a small triangular-shaped portion at the anterior end of the body, with a length on the dorsal side of 0.06, and on the ventral side of the body of 0.36 of the total length of the body, its greatest width being 0.53 transdiameter. The borders of the ventral portion converge posteriorly at an angle of 70°. The apex is truncate. The hypocone is broad with rounded sides and a broad, rounded, slightly notched antapex.

The girdle is placed far anteriorly, its distance from the apex being about 0.06 of the total length on the dorsal side of the body. On the ventral face both ends of the girdle turn posteriorly for a distance of 0.36 of the total length of the body and meet without displacement. The furrow is about 0.06 transdiameter in width, and deeply impressed with overhanging borders. The sulcus extends from the girdle to the antapex, wide at its beginning, contracted below and expanding as it nears the antapex, where it sometimes forms a deep notch. The transverse and longitudinal flagella arise near each other at the junction of the girdle and sulcus, probably from the same pore.

Nucleus and pusules are not figured by Herdman (1911*b*, *c*). The central part of the cytoplasm is occupied by a small, spherical body containing a central granule, from which radiate out to the periphery long, slender chromatophores (?), bright yellow in color. No striae recorded.

DIMENSIONS.—Length, 50$\mu$; transdiameter, 43$\mu$.

OCCURRENCE.—This species has been figured by Herdman (1911, 1912, 1913), from the Irish Sea at Port Erin, Isle of Man, from April to November. It occurred as greenish brown patches on the sandy beach, a little below high water mark, the largest of which was 50 yards long by 5 yards wide. None was found in the shallow waters offshore. These patches were present from a few days to a couple of weeks, when they would disappear to reappear several weeks later.

SYNONYMY.—It was described by Herdman (1911) as *Amphidinium operculatum* Clap. and Lach. It differs from that species, however, in its proportions, having a broader body, a wide, truncate apex, and a greater length in the epicone; it differs also in its coloring, which is bright yellow. It is therefore proposed as a separate species with the name *Amphidinium herdmani* nom. sp. nov.

COMPARISONS.—This species resembles *A. truncatum* (fig. U, 3) in its broad, truncate apex, but differs widely from it in all other respects. Its type of chromatophores is that of *A. operculatum* and *A. steini* (figs. U, 25, 28).

### **Amphidinium klebsi** nom. sp. nov.

Text figure U, 14

*Amphidinium operculatum,* Klebs (1884), pp. 723, 726, 732, 739, pl. 10, figs. 11, 12.
*A. operculatum,* Paulsen (1908), p. 96, fig. 128.

DIAGNOSIS.—A small species, with subcylindrical body, its length 1.72 transdiameters; girdle anterior; chromatophores (?). Length, 46μ. Bay of Naples, early spring months.

DESCRIPTION.—The body is subcylindrical (dorsoventrally compressed?), rounded posteriorly, subtruncate anteriorly with the middle portion drawn out in a slender tongue deflected to the left. The length of the body is 1.72 transdiameters at the widest part. The tongue-shaped portion at the anterior end is the epicone, which is separated from the rest of the body by the wide girdle. The exact limits of the girdle and epicone are not shown in Klebs's figures (1884). Its length above the base of the girdle is about 0.2 of the total length of the body, its width about 0.35 transdiameter. The hypocone is subcylindrical (flattened dorsoventrally?) with its sides subparallel for the middle third of their extent, rounded above and below. The antapex is broad and slightly rounded, while anteriorly the sides of the hypocone below the girdle swell forward and outward, forming wide, high shoulders, the left one narrower than the right.

The girdle is a wide circle embracing the narrow, necklike portion at the anterior end of the body. Its width is about 0.25 transdiameter. Its proximal border, as well as the sulcus, and the connections of girdle and sulcus are not indicated in Klebs's figures (1884). The longitudinal flagellum arises a short distance below the probable point of union of girdle and sulcus. The transverse flagellum arises in his figure on the right dorsal side of the body, a condition unparalleled in the dinoflagellates and one which is probably an error of drawing or interpretation.

The nucleus is a large, spherical body occupying the posterior half of the hypocone. Its axis is 0.43 transdiameter in length. The cytoplasm is filled with spherules of varying size and long, tapering chromatophores (?), which radiate forward and outward from the region of the nucleus in the posterior part of the body. The color of the organism is not noted by Klebs. The surface is apparently marked by a few longitudinal furrows or striae extending the length of the hypocone.

DIMENSIONS.—Length, 46μ; transdiameter, 28μ; axis of nucleus, 15μ.

OCCURRENCE.—Figured by Klebs (1884) from the Bay of Naples, where it appeared in large numbers in the early spring months.

SYNONYMY.—This form was figured by Klebs (1884) as *Amphidinium operculatum* Clap. and Lach. It differs from that species in its narrowly constricted girdle, tonguelike epicone, chromatophores radiating from the posterior end of the body and the furrows on its surface. It differs as widely from Herdman's (1911) and Stein's (1883) forms of the same species. It is therefore proposed to give it species rank with the name *Amphidinium klebsi* nom. sp. nov.

## **Amphidinium lacustre** Stein

Text figure U, 15

*Amphidinium lacustre* Stein (1883), p. 15, pl. 17, figs. 21–30.
*A. lacustre,* Bütschli (1885), pp. 940, 993, pl. 54, fig. 7.
*A. lacustre,* Pouchet (1885), p. 54.
*A. lacustre,* Schilling (1891), p. 62; (1913), p. 14, fig. 9.
*A. lacustre,* Mez (1898), p. 217.
*A. lacustre,* Ludwig (1898), p. 299.
*A. lacustre,* Schönichen and Kalberlah (1900), p. 230, pl. 8, fig. 2; (1909), p. 251, pl. 8, fig. 2.
*A. lacustre,* Lemmermann (1900), p. 115; (1903), p. 260; (1910), pp. 580, figs. 8–13, 616, 617.
*A. lacustre,* Zederbauer (1904), p. 2.
*A. lacustre,* Senft (1905), p. 89, figs. 42–48.
*A. lacustre,* Liebetanz (1905), p. 36; (1910), p. 42, pl. 2, fig. 39.
*A. lacustre,* Kofoid (1907*a*), p. 301.
*A. lacustre,* Entz (1907), p. 24; (1909), p. 262.
*A. lacustre,* Ohno (1911), p. 91.
*A. lacustre,* Herdman (1911*b*), p. 39; (1911*c*), p. 72.
*A. lacustre,* Francé (1912), p. 28.

Diagnosis.—A minute species with broadly ovoidal body, its length 1.25 transdiameters, antapex rounded; girdle anterior, without displacement; sulcus extending from girdle to antapex; brown chromatophores. Length, 23μ. Fresh water and brackish pools in Europe and Japan.

Description.—The body is rotund ovoidal, rounded posteriorly, almost flattened anteriorly, its length 1.25 transdiameters at the widest part. The epicone forms only a minute portion of the body, its length 0.13 of the total length of the body and its width about 0.52 transdiameter of the body. It forms a small rounded or somewhat flattened operculum-like lid separated from the rest of the body by the broad girdle. The hypocone is heart-shaped in ventral view, its length about 0.78 of the total length of the body, with a broad rounded antapex.

The girdle is anterior, forming a complete circle around the body about 0.13 of the total length of the body from the apex. The furrow is about 0.1 transdiameter in width, and deeply impressed. The sulcus is a furrow extending from the girdle to the antapex, wide anteriorly and narrowing posteriorly. A thickening occurs on the right border at the proximal end. Stein does not figure a transverse flagellum. The longitudinal flagellum arises at the junction of the girdle and sulcus at a point marked by the presence of a spherical pusule.

The cytoplasm contains numerous minute spherules and several larger brownish chromatophores. No nucleus has been figured by Stein.

Dimensions.—Length, 23μ; transdiameter, 18μ.

Occurrence.—Figured by Stein (1883) from fresh-water ponds and ditches near Prague, Austria. The only other records of its occurrence are those of Daday (Schilling, 1913, p. 14), who observed it in brackish pools near Déva, Hungary, and Liebetanz (1910), who records its appearance in the stomach contents (Panseninhalt) of four cows at Bern, Switzerland. All published figures subsequent to those of Stein (1883) appear to be based on those of that investigator.

COMPARISON.—This is probably the fresh-water representative of a marine species, *A. turbo*, both possessing some characteristics in common, the differences being probably due to the change in medium.

### **Amphidinium lanceolatum** Schröder

Text figure U, 9

*Amphidinium (?) lanceolatum* Schröder (1911), p. 650, fig. 15.
*A. lanceolatum,* Schiller (1912), p. 493.

DIAGNOSIS.—A small species with slender body, tapering posteriorly, its length 3.33 transdiameters; girdle far anterior; epicone minute, rounded, 0.33 transdiameter in width; sulcus not indicated; nucleus near center of body; cytoplasm filled with spherules of varying sizes; colorless. Length, 30 to 35μ; transdiameter, 9μ. Adriatic Sea near Rovigno, Austria.

Schröder (1911) questions the inclusion of this form with *Amphidinium.* His data, unfortunately, are very meager and need confirmation, but the minute size of the epicone, separated by the girdle from the elongated body, suggests the usual relations of these structures in *Amphidinium.* It is therefore placed in the genus, tentatively, until it has been found again and its structure more fully determined. Its proportions are suggestively like those of *Oxytoxum*, but there is no indication of a theca in either figure or description.

### **Amphidinium longum** Lohmann

Text figure U, 7

*Amphidinium longum,* Lohmann (1908), pp. 252, 201, 262, 366, 368, pl. 17, fig. 15; (1911), p. 31.
*A. longum,* Paulsen (1908), p. 96, fig. 131.
*A. longum,* Herdman (1911), pp. 71, 72; (1911), p. 38.
*A. longum,* Schröder (1911), pp. 625, 651.
*A. longum,* Lebour (1917*b*), p. 188.

DIAGNOSIS.—A minute species, with subovoidal body, its length 2.27 transdiameters; girdle anterior; epicone minute. Length, 25μ. Baltic Sea off Kiel, Germany, July, August; Adriatic Sea near Lucietta, Austria-Hungary.

DESCRIPTION.—The body is subovoidal, widest anteriorly behind the girdle, tapering slightly posteriorly, its length 2.27 transdiameters at the widest part. The epicone is a minute triangular portion with a sharply pointed apex, and a length of 0.12 of the total length of the body. The hypocone is broad anteriorly, tapering posteriorly to a narrow, rounded antapex.

Lohmann's figure (1908) shows what is apparently the dorsal side only, with no indication of the course of the remainder of the girdle and the sulcus. The girdle as figured is a broad (0.27 transdiameter), deeply impressed furrow extending transversely across the body at a distance from the apex of 0.12 of the total length of the body.

The nucleus is a small, ellipsoidal body found near the antapex. It is filled with fine chromatin granules. Its major and minor axes are about 0.55 and 0.36 transdiameters in length respectively. A spheroidal food mass is usually present near the girdle region.

DIMENSIONS.—Length, 25μ; transdiameter, 11μ; axes of nucleus, 6 and 4μ.

OCCURRENCE.—Figured by Lohmann (1908) from the Baltic Sea off Kiel in July and August. The only other record of its appearance is that of Schröder (1911) from the Adriatic Sea, near Lucietta off Austria-Hungary, July, in vertical hauls of 100 and 200 meters.

RELATIONSHIPS.—It stands midway between *A. lanceolatum* Schröder and *A. crassum* Lohmann (figs. U, 9, 18). Its form suggests *Oxytoxum*, but there is no indication of a theca.

## **Amphidinium operculatum** Claparède and Lachmann

Text figure U, 25

*Amphidinium operculatum* Claparède and Lachmann (1858–61), pp. 410, 411, pl. 20, figs. 9, 10.
*A. operculatum,* Leuckart (1861), p. 152.
*A. operculatum,* Diesing (1866), p. 97.
*A. operculatum,* Fromentel (1874), p. 197.
*A. operculatum,* Maggi (1874), p. 119; (1880), pp. 5, 15.
*A. operculatum,* Saville-Kent (1880–82), p. 461, pl. 25, figs. 45–46.
*A. operculatum,* Bergh (1882), p. 694.
*A. operculatum,* Daday (1883), p. 477; (1884), pp. 5, 11, 12.
*A. operculatum,* Entz (1884), p. 239; (1896), p. 22; (1904), p. 112; (1907), p. 18; (1909), p. 255.
*A. operculatum,* McIntosh (1889), pp. 323, 337.
*A. operculatum,* Balbiani (1894), p. 257, fig. 41.
*A. operculatum,* Levander (1894*c*), p. 210; (1910), p. 41; (1901*b*), pp. 8, 13, 18.
*A. operculatum,* Cleve (1894), p. 10.
*A. operculatum,* Schütt (1895), p. 92.
*A. operculatum,* Tempère (1898), p. 127, pl. 15, fig. 8. Indeterminable.
*A. operculatum,* Florentin (1899), p. 334.
*A. operculatum,* Lemmermann (1900), p. 115; (1901), p. 358; (1910), p. 616.
*A. operculatum,* Massart (1901), p. 81.
*A. operculatum,* Calkins (1902), p. 432, fig. 27.
*A. operculatum,* Kofoid (1907*a*), p. 301.
*A. operculatum,* Cavers (1913), p. 180, fig. $8_{4,\ 5}$.
*A. operculatum,* Griessmann (1913), pp. 3, 14.
Not *Amphidinium operculatum,* Stein (1883), Klebs (1884), Bütschli (1885), Schütt (1896), Schröder (1900), Lemmermann (1903), Paulsen (1908), Herdman (1911*a*, 1911*b*, 1912, 1913).

DIAGNOSIS.—A small species with ellipsoidal, dorsoventrally flattened body, its length 1.5 transdiameters; girdle anterior extending posteriorly on ventral side; sulcus extending from girdle to antapex; yellow brown chromatophores. Length, 45μ. Coast of Norway, west coast of Sweden, Atlantic off Woods Hole, Mass.

Description.—The body is broadly ellipsoidal in ventral view, narrowly so in side view, with broadly rounded apices, its length 1.5 transdiameters at the widest part. The epicone is a minute, triangular-shaped portion at the anterior end, its widest part about 0.4 transdiameter of the body, and its greatest length about 0.3 of the total length of the body. The hypocone is broadly rounded, narrowing slightly towards both ends.

The ends of the girdle meet at a point about 0.3 of the total length of the body from the apex. It passes anteriorly at an angle of about 20° from the main axis of the body, turns transversely across the dorsal side and thence posteriorly at an angle of about 25° with the main axis of the body. The furrow is wide and somewhat deeply impressed. The sulcus begins at the junction of the ends of the girdle and passes posteriorly to the antapex. The two flagella arise near each other at the point of junction of girdle and sulcus.

The nucleus has not been figured for this species by Claparède and Lachmann (1858–61) or by Calkins (1902). The central part of the body usually contains a small spheroidal body. Radiating from this out to the periphery are long chromatophores, yellow brown in color.

Dimensions.—Length, 40 to 50$\mu$; transdiameter, 30$\mu$; dorsoventral diameter, 15$\mu$.

Occurrence.—Figured by Claparède and Lachmann (1858–61) from collections made along the coast of Norway. Other records of its occurrence are as follows: Entz (1896) from salt pools near Dèva, Hungary, and Cleve (1894) along the west coast of Sweden, Calkins (1902) at Woods Hole, Mass., Massart (1901) in pools and ditches near Palingbrug, Belgium, and Griessmann (1913) in laboratory cultures from sea water at Roscoff, France. No figures or descriptions are given by Massart and Griessmann; hence the identity of their forms must be held in doubt.

## **Amphidinium ovoideum** Lemmermann

Text figure U, 19

*Prorocentrum ovoideum* Lemmermann (1896*b*), p. 147, figs. 1–3; as *Amphidinium ovoideum,* (1900), p. 115; (1902), p. 260; (1910), p. 616, fig.
*Amphidinium ovoideum,* Paulsen (1908), p. 96.
*A. ovoideum,* Klebs (1912), p. 438.

Diagnosis.—A minute species with broad, oval body, its length 1.25 transdiameters; girdle far anterior; sulcus (?); brown chromatophores. Length, 23$\mu$. Brackish water, near Baltic Sea, Germany.

Description.—The body is broadly oval to rounded, with broad apices, its length 1.25 transdiameters at the widest part. The epicone is minute, its length from the distal border of the girdle, 0.12 of the total length of the body and its greatest width 0.38 transdiameter. The apex is broadly rounded. The hypocone is symmetrical, tapering at both ends, with broad, round antapex.

Lemmermann's figures (1896*b*) give only what is apparently the dorsal side, hence the complete course of the girdle and the sulcus cannot be traced. The girdle passes transversely across the dorsal side at a distance from the apex of 0.12 of the total length of the body.

The nucleus is a spheroidal body found near the antapex. Its axis is about 0.38 transdiameter in length. The body is filled with closely crowded, spherical, brown chromatophores. No striae are recorded.

DIMENSIONS.—Length, 17–23μ; transdiameter, 17–21μ; axis of nucleus, 5μ.

OCCURRENCE.—Figured by Lemmermann (1896*b*) from brackish, stagnant water along the borders of the Baltic Sea near Plön, Germany.

SYNONYMY.—This form was first described by Lemmermann (1896*b*) as *Prorocentrum ovoideum* and the name afterwards (1900) changed to *Amphidinium ovoideum*. Paulsen uses it as a synonym of *Amphidinium operculatum* Clap. and Lach. In this, however, he is evidently mistaken, as a glance at the two figures (text figs. U, 19, 25) will show. It differs in size and proportions, and particularly in the size and shape of the chromatophores. These Lemmermann (1910) found were constant in his cultures and concluded that it formed a valid species.

## **Amphidinium pacificum** sp. nov.

Plate 2, figure 13; text figure U, 24

DIAGNOSIS.—A large species with ellipsoidal body, its length 1.75 transdiameters, girdle without displacement; sulcus extending from girdle to antapex; pyrite yellow chromatophores. Length, 93μ. Pacific off La Jolla, California, July.

DESCRIPTION.—The body is ellipsoidal with broad, rounded apices, nearly circular in cross-section, its length 1.75 transdiameters at the widest part. The epicone occupies a relatively small part of the body, its distance from the apex on the dorsal face being only 0.03 of the total length of the body. On the ventral face it extends posteriorly for about 0.49 of the total length of the body, its sides forming an angle of about 60°. Its greatest transdiameter is about 0.14 of the greatest transdiameter of the body. The hypocone is broad, slipper-shaped, widest in the middle and flaring slightly immediately behind the girdle. The antapex is broad and rounded.

The girdle and sulcus meet at a point distant from the apex 0.49 of the total length of the body. It turns anteriorly at an angle of 30° with the longitudinal plane of the body, for a short distance, beyond which it steepens until near the margin it becomes subparallel with the main axis. On the dorsal face it follows an almost transverse direction across the body, 0.03 of the total length of the body from the apex, turning posteriorly on the right ventral face at an angle of about 30° with the main axis and meeting the anterior end of the sulcus without displacement. The furrow is about 0.05 transdiameter in width, and deeply impressed, with smooth, slightly undercut borders. The sulcus extends from the girdle to the antapex as a narrow, somewhat obscure furrow. The anterior flagellar pore is found at the junction of the two ends of the girdle.

The nucleus is a broadly ellipsoidal body on the right side of the middle part of the hypocone. Its major and minor axes are about 0.47 and 0.34 transdiameters in length respectively.

A small sacklike pusule opens into the anterior flagellar pore. The cytoplasm is finely granular and is filled with large alveoli. Near the anterior flagellar pore is a group of minute, dark green, refractive granules, mingled with which are a few blue green spherules. In the peripheral zone are a few ellipsoidal, leaflike chromatophores, pyrite yellow in color. These are most numerous along the lateral margins of the body and near the girdle.

DIMENSIONS.—Length, 93μ; transdiameter, 53μ; axes of nucleus, 25 and 18μ.

OCCURRENCE.—This was taken July 25, 1917, in a surface haul 11 miles off La Jolla, California, in a surface temperature of 21°75 C.

COMPARISONS.—This is the only one of the larger species of *Amphidinium* which possesses the small leaflike chromatophores such as are found in *A. dentatum* and *A. galbanum* (figs. U, 4, 29).

### **Amphidinium rotundatum** Lohmann

Text figure U, 22

*Amphidinium rotundatum* Lohmann (1908), pp. 147, 199, 202, 254, 261, 324, table B, pl. 17, fig. 9; (1911), pp. 30, 31, fig. 12*c*, pl. 1, fig.5

*A. rotundatum,* Paulsen (1908), p. 95, fig. 129.

*A. rotundatum,* Herdman (1911*b*), p. 71; (1911*c*), p. 38.

*A. rotundatum,* Schiller (1911), p. 31.

*A. rotundatum,* Mielck (1914), p. 20.

*A. rotundatum,* Ostenfeld (1913), p. 338.

*A. rotundatum,* Lemmermann (1910), p. 615.

DIAGNOSIS.—A minute species with broadly ovoidal body, its length 1.2 transdiameters; epicone very minute; yellow chromatophores. Length, 12μ. Baltic Sea off Kiel, Germany.

DESCRIPTION.—The body is broadly top-shaped, the narrow neck and head formed by the girdle and flat epicone tapering posteriorly to a blunt antapex. Its length is 1.2 transdiameters at the widest part. The girdle is broad, about 0.25 transdiameters, and deeply constricts the anterior part of the body to 0.5 of its width behind the girdle. Sulcus not known. The flat epicone also has a width of 0.5 transdiameter and no appreciable length. The most striking thing about this organism is the yellow, leaflike chromatophores located in the peripheral layer of the cytoplasm.

DIMENSIONS.—Length, 12μ; transdiameter, 10μ.

OCCURRENCE.—Figured by Lohmann (1908) from the Baltic Sea off Kiel, Germany, present throughout the year. Mielck (1914) records its presence in the Barents Sea and White Sea near Kola, Russia, in June and July.

### **Amphidinium scissum** sp. nov.

Plate 2, figure 22; text figure U, 1

DIAGNOSIS.—A small species with ovate body, compressed dorsoventrally to 0.5 transdiameter, wider posteriorly; epicone flattened, higher at the right; hypocone deeply notched at antapex; girdle displaced posteriorly 0.24 transdiameter; sulcus runs from apex to antapex; color greenish; food inclusions often present; littoral habitat. Length, 56μ. Pacific at La Jolla, California, July.

DESCRIPTION.—The body is ovate, its greatest transverse diameter 1.7 to 1.8 transdiameters at its widest part, which is slightly below the middle, compressed dorsoventrally to little less than 0.5 the greatest transdiameter. Its length is about 3 transdiameters measured in the girdle. The

length of the epicone is about 0.16 of the total length, measured from the proximal end of the girdle; its transdiameter, measured on the anterior lip of the girdle, is about 0.6 the greatest transdiameter of the hypocone, and its dorsoventral diameter about 0.33 of the same. The apex is flattened and slopes to the right at an angle of 15° to 17° from the horizontal. It is traversed by the sulcus, which crosses the apex and swings around to the left, encircling a small terminal button, somewhat as in some species of *Pouchetia*. The hypocone is broadly ellipsoidal, its greatest length, on its left shoulder, about 1.5 its greatest diameter, which is located about midway between girdle and antapex. Dorsoventrally it is widest at 0.33 of its length from the antapex, expanding gradually from the girdle, where its dorsoventral diameter is 0.66 of the diameter at its widest part, and contracting at the antapex to an almost hemispherical outline in lateral view, broken, however, by the deep semicircular notch at the posterior end of the sulcus. This notch is about three times the width and depth of the girdle. It lies a little to the right of the main axis and the left margin is the larger and longer one.

The girdle forms a descending left spiral, deepest at its ends, both of which are sharply deflected posteriorly at angles of 30° and 45° respectively at the proximal and distal regions. The distal displacement posteriorly is about twice the width of the girdle. There is no overhang. The furrow is deeply impressed with broadly rounded lips. The transverse flagellum completely encircles the body.

The sulcus runs the whole length of the body, terminates anteriorly in a sinistral loop around an apical button, has a slight sigmoid curve at the girdle and flares posteriorly in the antapical notch. A ventral lobe on the right side at the posterior end pushes it somewhat to the left. The longitudinal flagellum extends from the flagellar pore near the posterior end of the sulcus posteriorly beyond the antapex for a distance equal to the length of the body.

The surface is minutely and faintly striate with equidistant, parallel, longitudinal lines, about eighteen across the dorsal face. They show faintly on the epicone, but more clearly on the hypocone.

The cell contents consist of the posteriorly located ellipsoidal nucleus and numerous peripheral greenish spherules of high refractive index, probably fatty products of metabolism. No definite chromatophores could be detected. The whole body has a pale, sea foam green tone, due in part at least to the refractive bodies. All inclusions in the form of yellowish spheres, red, and orange spherules in different individuals are indications of the holozoic nutrition of this organism.

Luminescence not observed.

DIMENSIONS.—Length of body, 56μ; transdiameter in girdle, 20μ; at widest part, 32μ; dorsoventral, 18μ.

OCCURRENCE.—Taken frequently in washings from beach sand on ocean shore at La Jolla, California, in July, 1914.

COMPARISONS.—This species is referred to *Amphidinium* rather than *Gymnodinium* because of its reduced epicone, deeply incised sulcus, and dorsoventral compression. The large size of the epicone allies it with *Gymnodinium*, but this feature is shared with *Amphidinium asymmetricum*, *A. sulcatum*, *A. corpulentum* and to some extent with *A. truncatum* (figs. U, 5, 10, 6, 3). The extension of the sulcus upon the epicone is also a feature of *A. corpulentum* and *A. sulcatum*. Linear striae have been recorded in *Amphidinium* only on this species and *A. asymmetricum* and *A. truncatum*.

### **Amphidinium steini** Lemmermann

Text figure U, 28

*Amphidinium operculatum* Stein (1883), p. 16, pl. 17, figs. 7–20.
*A. operculatum,* Pouchet (1883), p. 427; (1885*a*), pp. 32, 50, 51, 53, 54, 82, 83, 86, pl. 2, fig. 9.
*A. operculatum,* Bütschli (1885), pp. 958, 967, 968, 1026.
*A. operculatum,* Schütt (1896), p. 4, fig. 4.
*A. operculatum,* Schröder (1900), p. 13.
*A. operculatum,* Lemmermann (1902), p. 260; as *Amphidinium steinii,* (1910), pp. 580, 616, figs. 1–7.

Diagnosis.—A small species with asymmetrical ovoidal, dorsoventrally compressed body, its length 1.73 transdiameters; girdle anterior, without displacement; sulcus extending from girdle to antapex; brown chromatophores. Length, 45μ (?). Brackish waters, Wismar, Germany.

Description.—The body is asymmetrical, broadly ovoidal in ventral view, widest anteriorly, dorsoventrally compressed with the ventral side convex and the dorsal convex anteriorly, but concave posteriorly. Its length is 1.73 transdiameters at the widest part and its dorsoventral diameter 0.63 transdiameter. The epicone is a minute, caplike portion, separated from the rest of the body by the wide girdle which abruptly constricts the anterior part of the body. Its length is 0.16 that of the hypocone and its width 0.38 transdiameter. It is almost circular in outline, slightly rounded, and obliquely placed on the body so that the left dorsal side is much higher than the right ventral side. The greater convexity of the right and ventral sides of the body throws the epicone and girdle somewhat to the left and dorsal of the main axis. The hypocone is long heart-shaped in ventral view, asymmetrical with the right side more convex than the left, and with rounded antapex.

The girdle is placed far anteriorly and forms a complete circle about 0.3 transdiameter in width. It deeply constricts the anterior part of the body, which, on its distal border, forms wide, squarish shoulders, with the proximal border narrow and smoothly rounded. Dorsad its distance from the apex is about 0.05, and ventrad 0.16 of the total length of the body. On the ventral face of the body it merges into the wide V-shaped anterior end of the sulcus. The sulcus narrows to a slender line posteriorly and terminates without sulcal notch near the antapex, and is usually deflected slightly to the left near its posterior end. The longitudinal flagellum arises at the junction of the girdle and sulcus.

The nucleus is a small, spherical body found in the posterior half of the hypocone. Its axis is about 0.34 transdiameter. At the junction of girdle and sulcus is a small, spherical pusule, probably connected with the flagellar pore. In the central part of the cytoplasm is a small, spheroidal amyloid (?) body and radially arranged around this are small stout rod-shaped brown chromatophores. Three individuals showing the presence of ingested food bodies are figured by Stein (1883, pl. 17, figs. 14–16. The chromatophores in these are smaller than in his figures 12 and 13. This would lead to the conclusion that nutrition may be either holozoic or holophytic in this species.

Dimensions.—These are only approximate, as Stein (1883) gives neither dimensions nor exact magnifications for his figures. Length, 45μ; transdiameter, 26μ; axis of nucleus, 9μ.

Occurrence.—Figured by Stein (1883) from brackish water near Wismar, Germany.

SYNONYMY.—This was originally figured by Stein (1883) as *Amphidinium operculatum* Clap. and Lach. and separated as *A. operculatum* var. *steini* by Lemmermann (1910).

### Amphidinium sulcatum Kofoid

Text figures U, 10, 26

*Amphidinium sulcatum* Kofoid (1907*a*), pp. 299, 300, pl. 22, figs. 1–3.
*A. sulcatum,* Lemmermann (1910), p. 615.
*A. sulcatum,* West (1916), p. 52, fig. 37.
*A. sulcatum,* Herdman (1911*b*), p. 72; (1911*c*), p. 39.

DIAGNOSIS.—A rather large, laterally compressed species, its length 1.7 transdiameters; girdle anterior; sulcus extending from apex to antapex; small yellow chromatophores. Length, 68$\mu$. Pacific off San Diego, June.

DESCRIPTION.—The body is laterally compressed, broadly oval in lateral view, ellipsoidal in ventral view. Its length is 1.7 transdiameters, the dorsoventral diameter 1.4 transdiameters at the widest part. The greatest width of the body is midway between the girdle and antapex. The epicone is minute compared with the hypocone, its length being 0.14 of the total length of the body. It is highest laterally and dorsally and hollowed out towards the sulcus, which passes dorsally beyond the apex. The hypocone is broadly rounded posteriorly, and very deeply channeled ventrally by the sulcus, which deepens as it passes posteriorly from the flagellar pore.

The girdle is anterior in position, slightly enlarged on the left side and narrowed at its distal end, which is displaced posteriorly by about the width of the proximal end of the furrow. The furrow is very deeply imbedded and its proximal width is more than twice that of the distal region. The sulcus extends from the dorsal half of the epicone to the antapex. It is a narrow channel anteriorly with a depth at the flagellar pore of 0.25 of the dorsoventral diameter at that level and deepens posteriorly until at the antapex it reaches nearly 0.5 of the dorsoventral diameter. The right lip of the furrow is somewhat higher than the left.

The surface is covered with a thin hyaline membrane. The nucleus is a spheroidal body in the middle of the hypocone. It is filled with moniliform chromatin strands and two polar centrosomes (?) or nucleoli sunk in its substance. A pyriform vacuole lies near the flagellar pore, but its connection with the opening is not evident. A large amyloid body is present near the nucleus and surrounding it are small angular yellowish chromatophores. The cytoplasm is dense and coarsely granular.

DIMENSIONS.—Length, 68$\mu$; transdiameter, 35$\mu$; dorsoventral diameter, 55$\mu$; diameter of nucleus, 15$\mu$.

OCCURRENCE.—Taken in a vertical haul of 165 meters to the surface, 10.5 miles off San Diego, California, June 14, 1904.

COMPARISONS.—This species stands alone among the species of *Amphidinium* in having a laterally compressed body. It is, however, tentatively placed with the dorsoventrally compressed forms in the subgenus *Amphidinium*. Possibly a separate subgenus should be established for the species. The truncate anterior end recalls the condition in *A. herdmani* and *A. truncatum*.

### **Amphidinium truncatum** sp. nov.

Text figure U, 3

DIAGNOSIS.—A small species with sacklike body, its length 1.2 transdiameter, dorsoventrally compressed to 0.5 transdiameter; epicone low, squarely truncate, left antapex pointed; sulcus confined to striate hypocone; pale green; littoral habitat. Length, 38μ. Pacific at La Jolla, California, July, August.

DESCRIPTION.—The body is stout, its length 1.2 transdiameter, dorsoventrally compressed to 0.5 transdiameter. The epicone is 0.2 of the total length in height, and squarely truncate. Its form above the girdle is that of a very low, truncate, ellipsoidal cone, whose major and minor axes in its base are respectively 0.67 and 0.33 transdiameter and truncate apex 0.50 and 0.25 respectively. Its short side has a slope of about 40°. There is a noticeable suppression of the asymmetry of the epicone so characteristic of *A. asymmetricum* and *A. operculatum*. The hypocone is rotund, its length 0.8 of the total length and about equal to its greatest transdiameter which is located near the middle. Its left side is less convex than the right and it shares with the epicone the considerable dorsoventral compression. Anteriorly it spreads abruptly below the girdle in a squarish shoulder, thereby increasing the width (transversely) at that level 25 per cent more than that of the epicone. The antapex is broadly rounded with a low symmetrical rounded part on the right side of the deeply excavated posteriorly flaring sulcus, and a sharp point on the left which projects less than a furrow's width beyond the general contour.

The girdle is symmetrical, located 0.12 of the length below the apex. Its course is nearly horizontal except at its proximal and distal ends which form an almost symmetrical V-shaped junction on the ventral face about as long as the epicone. The furrow is broad, 0.12 transdiameter, and shallow. The sulcus is confined in the hypocone, is about two-thirds the width of the girdle, has a very slight sigmoid curvature and widens posteriorly to 0.2 transdiameter. It is deeply excavated to the middle of the body posteriorly at a point just below the junction of the ends of the girdle. It has no flap on its left side, but is open throughout its course. Both margins are continued beyond the antapex in a short projecting, more or less pointed tooth, the left being the longer. The longitudinal flagellum arises from a pore at the proximal end of the sulcus, just behind the anterior flagellar pore. It extends posteriorly beyond the body for 0.83 of the total length.

The surface is uniformly striated on the hypocone with equidistant, parallel faint lines, about twenty across the dorsal face. No lines can be detected on the short slopes of the epicone. The peripheral pellicle surrounding the body is very distinct. The nucleus is an ellipsoidal, subreniform body located in the left posterior part of the hypocone with its long axes passing from the left anteriorly, to the right posteriorly. It is a little more than 0.5 of the transdiameter in length, its minor axis is a trifle more than 0.5 of the major, and it shares in the general dorsoventral compression. A large pusule opens into the anterior flagellar pore and is connected by a narrow canal with a smaller, circular pusule farther posterior and on the right side of the body. A halo of subspheroidal, bluish green chromatophores fills the peripheral layer of cytoplasm. The general color is a diffuse pale pea green.

DIMENSIONS.—Total length, 38μ; greatest transdiameter, 30μ; dorsoventral diameter, 15μ.

OCCURRENCE.—Very abundant in the beach sand off La Jolla, California, during July, 1914. It lives in laboratory aquaria for two to three days, but becomes inactive very quickly when exposed to the illumination of the microscope.

COMPARISONS.—The flattened epicone of this species suggests those of *A. operculatum*, *A. scissum*, and *A. herdmani* (figs. U, 25, 1, 2), the last having the greatest resemblance. It is quite distinct from these species, however, in the form of epicone, the well developed pellicle, proportions of the body, and the striate hypocone.

## **Amphidinium turbo** sp. nov.

Plate 9, figure 98; text figure U, 16

DIAGNOSIS.—A minute species with broadly ovoidal body; length 1.38 transdiameters, apex and antapex subacute; girdle anterior without displacement; sulcus very short; color pearl grey. Length, 23$\mu$. Pacific off La Jolla, California, July.

DESCRIPTION.—The body is broadly ovoidal, widest in front of the middle part of the body, its length 1.38 transdiameters at the widest part. The epicone is a minute peaked, caplike portion surmounting the broad girdle. It has a length of 0.13 of the total length of the body. It is broadly conical in shape, forming an angle of about 110°, with the apex excentrically placed slightly to the left. The hypocone is cordate-shaped in ventral view and symmetrically rounded, with slight tendency to a subacute point at the antapex.

The girdle is broad, about 0.15 transdiameter and deeply impressed. It is placed far anteriorly and the transdiameter in it is about 0.4 of the broadest transdiameter of the body. It forms a complete circle around the body. The anterior flagellar pore is located near the posterior border of the girdle at the left of the median line. The posterior pore is located about one width of the girdle below the anterior one. The sulcus is a short V-shaped depression below the anterior flagellar pore. Its length is nearly twice the diameter at the girdle.

The large, spheroidal nucleus is found in the central part of the body. Coarse moniliform chromatin strands, eight across one face, are prominent in its structure. Its axis is about 0.5 transdiameter in length.

The cytoplasm is very clear and transparent without apparent granulations. Its color is pearl grey. The pellicle of the hypocone appears as a double-contoured line. The cytoplasm contains numerous, blue green spherules and more minute granules. The epicone appears to be destitute of these. No striations or other markings could be detected on the surface.

DIMENSIONS.—Length, 23$\mu$; transdiameter, 17$\mu$; axis of nucleus, 9$\mu$.

OCCURRENCE.—Two individuals were observed in the collections made in the Pacific off La Jolla, California, in 1917. These were taken July 5, with a No. 12 silk net, in a haul 6 miles off La Jolla, from 80 meters to the surface and in a surface temperature of 21°9 C. On July 25 another was noted in a haul made 11 miles offshore, from 80 meters to the surface and in a surface temperature of 21°7 C.

COMPARISONS.—This form shows a strong resemblance to *A. lacustre* Stein. Stein's (1883) species is found in fresh and brackish waters and possesses brownish chromatophores. It may be that our form is the marine representative of the same species.

## **Amphidinium vasculum** sp. nov.

Text figure U, 27

Diagnosis.—A rather large species with subcuneiform body, its length 1.54 transdiameters; girdle without displacement; sulcus short on epicone, reaching antapex on hypocone; color, bright green mixed with pink and yellow orange. Length, 94μ. Pacific, off La Jolla, California, August.

Description.—The body is rotund, subcuneiform, broadly rounded posteriorly, conical anteriorly, where is also its widest part; its length is 1.54 transdiameters at the widest part. A cross-section of the body is nearly circular in outline. The epicone occupies a relatively small part of the body. Viewed from the ventral face it is rhomboidal in shape, with its greatest length equal to 0.4 of the total length of the body. Dorsad, the length of the epicone is 0.13 of the total length. Its general shape is that of a broad, flat cone of 122° with blunt apex, and nearly straight sides. The hypocone is elongate cylindrical, flaring somewhat anteriorly and broad, smoothly rounded posteriorly, a trifle longer at the left.

The girdle joins the sulcus at a distance from the apex of 0.4 of the total length of the body. It immediately turns anteriorly at an angle of about 50° with the longitudinal axis of the body, with a slight irregularity in its course, until it reaches the dorsal side of the body, which it traverses in an almost transverse direction at a distance from the apex of 0.13 of the total length of the body. On the right side of the ventral face it again turns posteriorly at an angle of 55° and meets the opposite end of the sulcus without displacement. The furrow is wide, about 0.05 transdiameter, and deeply impressed, undercutting its anterior border and curving gradually outward posteriorly. Both lips are smooth and flare slightly beyond the surface of the body. The sulcus begins about midway between its junction with the girdle and the apex and extends posteriorly to the antapex. Its course on the epicone is at an angle of about 25° with the longitudinal axis of the body. Beyond the girdle its course is that of a straight line to the posterior margin of the body. Posterior to the anterior flagellar pore it becomes slightly narrower than on the epicone, broadening at its posterior extremity. The anterior flagellar pore is located at the junction of the girdle and sulcus, the posterior pore about midway between that and the antapex.

The nucleus is a rather large ovoidal body lying slightly posterior to the central part of the hypocone. Its axis is about 0.44 transdiameter in length. A small sacklike pusule opens into each flagellar pore. The cytoplasm is finely granular and shows a distinct line of ectoplasm around the margin of the body. This is clear and devoid of alveoli or other markings. In the central part of the cytoplasm, slightly posterior to the anterior flagellar pore, is a dark, spheroidal body, ventrad to which is a group of minute, bright green refractive granules. These immediately surround the anterior flagellar pore and its communicating pusule. Radiating out from this center are a number of long, blue green rodlets or canals. Near both apices are groups of large, salmon pink vacuoles. A few blue green oil droplets and one large, olive green body and one of yellow ochre near the midregion complete the list of cytoplasmic inclusions. The general color is bright green mixed with pearl grey, pink and yellow orange. No striae or other surface markings could be detected.

Dimensions.—Length, 94μ; transdiameter, 61μ; axis of nucleus, 28μ.

Occurrence.—This was found August 6, 1917, in a haul 4 miles off La Jolla, California, with a No. 25 net, from 60 meters to the surface and in a surface temperature of 21.2 C. It was observed again on August 13, in a haul 0.75 mile offshore and from 83 meters to the surface.

COMPARISONS.—This species greatly resembles *Gymnodinium amphora.* The relative proportions of epicone and hypocone, however, tend to rank it with *Amphidinium,* though on rather arbitrary grounds. It and *A. cucurbita* are the most highly specialized members of the genus and of a type closely paralleling the highest specialization of the genus *Gymnodinium.* The ectoplasmic structure in *A. vasculum* lacks the high degree of development found in many of the species of the subgenus *Pachydinium* in *Gymnodinium,* but is clearly of a similar nature. In its cytoplasmic structure it resembles *A. cucurbita* and *Gymnodinium dogieli* and *G. pachydermatum.* In coloring it is one of the most striking species of the genus.

CHAPTER XI

# GYMNODINIIDAE: GYMNODINIUM, G. ABBREVIATUM TO G. GRAMMATICUM

## **GYMNODINIUM** Stein emend.

Text figures A, B, I, M, V–BB

*Gymnodinium* Stein (1878–83), in part, pp. 89–91, pl. 2, figs. 14–21, pl. 3, figs. 1–4.
*Peridinium* Ehrenberg (1834), in part, pp. 126–127; (1835), pp. 270–271; (1838), p. 254, pl. 22, fig. 15.
*Gymnodinium,* Saville-Kent (1880–82), pp. 442–444, pl. 25, figs. 17–20, 53, 54, 58–61.
*Gymnodinium,* Pouchet (1883), in part, pp. 445, 446, text figs. I, L, M, pl. 21, figs. 39, 40.
*Gymnodinium,* Bütschli (1885), in part, pp. 1007, 1008, pl. 51, figs. 4–9.
*Gymnodinium,* Schütt (1895), in part, pls. 21–25; (1896), pp. 4, 5, fig. 5.
*Gymnodinium,* Delage and Hèrouard (1896), in part, p. 384. Fig. 666 is *Gyrodinium spirale.*
*Gymnodinium,* Mez (1898), in part, p. 216.
*Gymnodinium,* Schönichen and Kalberlah (1900), p. 230; (1908), p. 251.
*Gymnodinium,* Calkins (1902), in part, p. 429, fig. 20.
*Gymnodinium,* Paulsen (1908), in part, pp. 97–101, figs. 132–138.
*Gymnodinium,* Lemmermann (1910), p. 565, figs. 13, 14, 17–23; p. 613, figs. 1–19, 23, 26, 30; pp. 618–626.
*Gymnodinium,* Doflein (1911), in part, pp. 526–529, figs. 472–475.
*Gymnodinium,* Poche (1913), pp. 162, 163.
*Gymnodinium,* Schilling (1913), pp. 14–21, figs. 10–20.

### Diagnosis

Gymnodiniidae without torsion of the body; girdle a descending left spiral displaced less than one-fifth the total length of the body or it may form a complete circle around the body; sulcus may extend from the apex to the antapex or may be very short on either epicone or hypocone or both. The nucleus is usually in the center or posterior part of the body, but is sometimes found anteriorly; perinuclear membrane rarely present; nucleus usually filled with distinct moniliform chromatin strands. Pusules are generally found, opening anteriorly into the anterior flagellar pore, posteriorly into the posterior pore, or rarely they may be fused into one large pusule opening into both pores. No nematocysts; plasma varying from colorless, with or without chromatophores, to highly colored; pigment granules sometimes present. Surface may be smooth, striate, ridged, or furrowed. Sometimes differentiated into ectoplasm and endoplasm. Nutrition may be holozoic or holophytic. Encystment in thin-walled membrane frequent. Length, 11–210$\mu$. Marine, brackish, and fresh waters, pelagic and littoral, mainly in temperate latitudes; 76 species known.

## Organology

*Gymnodinium* stands next to *Amphidinium* in its organology, differing mainly from that genus and from *Gyrodinium* in the position and arrangement of girdle and sulcus. The epicone occupies a relatively greater proportion of the body than in *Amphidinium*, the girdle being placed nearer the center of the body (fig. V). A few species, as for example *G. amphora* (fig. AA, 6), approach the *Amphidinium* type. The girdle may form a complete circle around the body, as in *G. lineopunicum* (fig. X, 17), or the ends may be displaced from a very slight amount up to nearly 0.2 of the total length of the body. A displacement as great as this is rare, *G. rubrum* alone showing it (fig. Y, 4). When so displaced the girdle approaches the *Gyrodinium* type. It is usually submedian or slightly anterior in position. Three species only exhibit, in a noticeable degree, a location of the girdle posterior to the equator or middle of the body, *G. dissimile, G. musei,* and *G. vorticella* (figs. X, 32, 3, 29).

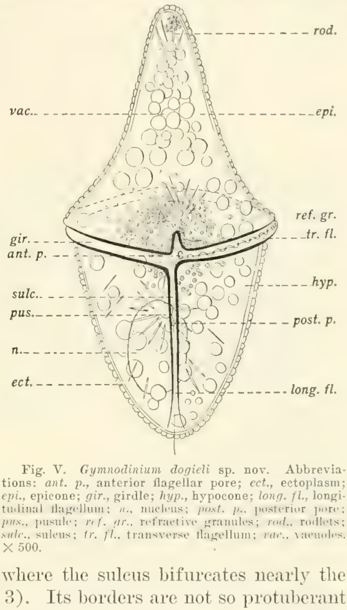

Fig. V. *Gymnodinium dogieli* sp. nov. Abbreviations: *ant. p.*, anterior flagellar pore; *ect.*, ectoplasm; *epi.*, epicone; *gir.*, girdle; *hyp.*, hypocone; *long. fl.*, longitudinal flagellum; *n.*, nucleus; *post. p.*, posterior pore; *pus.*, pusule; *ref. gr.*, refractive granules; *rod.*, rodlets; *sulc.*, sulcus; *tr. fl.*, transverse flagellum; *vac.*, vacuoles. × 500.

The sulcus is usually well developed, without torsion or with only a very slight amount, as in *G. rubrum*. It usually extends from or near the apex to the antapex in a more or less sinuous line. It is shallow anteriorly, generally deepening posteriorly, its greater development in the latter respect being reached in *G. bifurcatum,* where the sulcus bifurcates nearly the entire length of the hypocone (fig. AA, 3). Its borders are not so protuberant as in *Amphidinium*, yet are apparently capable of great distension, as shown by the size of the food bodies sometimes ingested (pl. 6, fig. 65).

The position of the nucleus is not constant, but it may be found in any part of the body. This sometimes happens within the species, as in *G. heterostriatum*, as a result of the ingestion of large food masses which displace the existing cell contents. In the greater number of species it is found in the central or posterior parts of the body. It usually has distinct, beaded chromatin threads. One species only, *G. rubrum* (pl. 8, fig. 86), shows a well developed, perinuclear membrane. This is similar in its structure to that found in *Gyrodinium corallinum* (pl. 10, fig. 117). It is noteworthy also that this species stands nearest to *Gyrodinium* in its type of girdle arrangement.

In cytoplasmic differentiation, as distinct from the organelles contained within it, the genus *Gymnodinium* exhibits both the simplest as well as the most advanced conditions found within the Gymnodiniidae, if not indeed within the Gymnodinioidae. The simplest type is shown in *G. minor* with its minute protoplasmic body surrounded by a thin periplast (fig. X, 12). The most advanced type is that found in *G. dogieli*, with its thickened ectoplasm consisting of two distinct layers completely surrounding the body and its distinct groups of vacuoles, refractive bodies and radial rodlets, and its well developed pusules (fig. V). Its ectoplasm resembles that in many of the ciliates, the alveolar layer, however, being at the surface of the body instead of separated from it by a layer as is usual with the Ciliata. The superficial location of the alveoli gives a bossed surface to these organisms which is very characteristic.

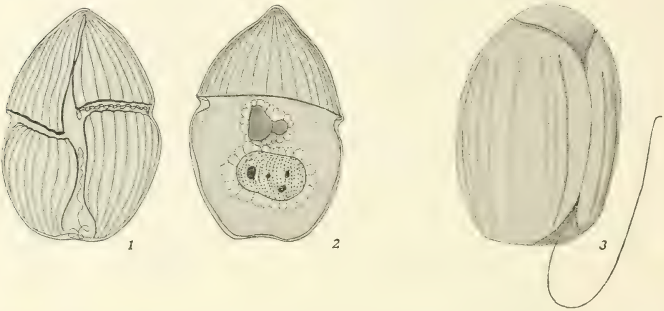


Fig. W. 1, 2. *Gymnodinium lira* sp. nov. × 477. 1. External form only, showing the ridges of the body. 2. Optical section of hypocone showing the structure of the cytoplasm. Note vacuoles surrounding nucleus and the food body. 3. *Amphidinium cucurbita* sp. nov. × 500. Superficial structure of the body only, showing the furrows and striations of the surface.

The surface of the body in *Gymnodinium* presents nearly all the modifications found within the Gymnodinioidae. In the subgenus *Gymnodinium*, containing the primitive or more generalized species, surface striae or other markings are relatively rare (fig. X). One species in that group, *G. herbaceum* (fig. Y, 17), shows a few, rather widely separated striae on the hypocone only; *G. sulcatum* has the hypocone marked by a few furrows, and *G. contractum* the same markings on the epicone. In the subgenus *Lineadinium* (fig. Y) each species shows a typical and fairly constant striate surface. The striae may be distinct lines or linear series of short rodlets, and usually vary somewhat in number on epicone and hypocone. In all the species carefully observed these striae are blue green, as are also those in the next subgenus. When pigment is present it is found to collect along the surface striae as in *G. rubrum* (pl. 8, fig. 85). This is a condition more frequently met with, however, in *Gyrodinium*.

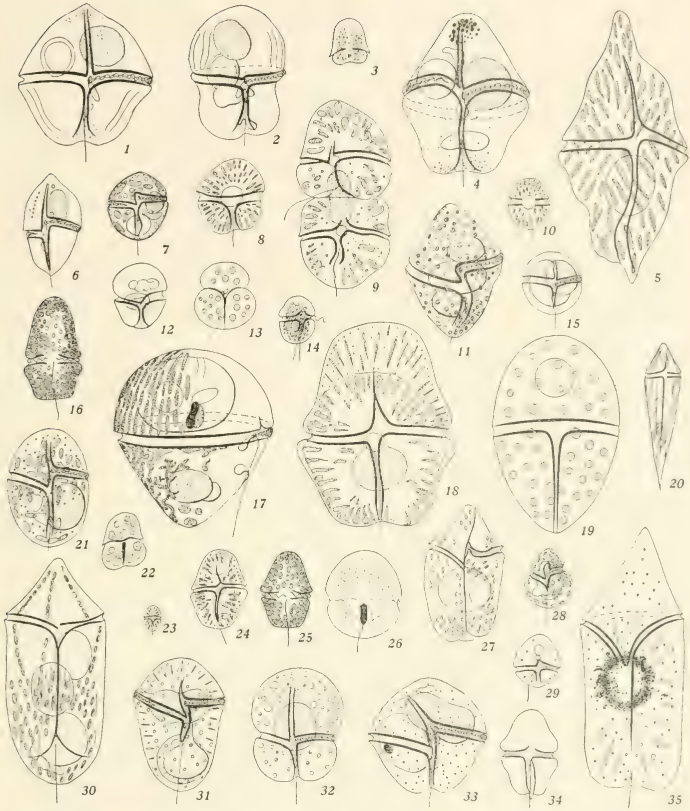

Fig. X. *Gymnodinium,* subgenus *Gymnodinium* subgen. nov. 1. *G. sulcatum* sp. nov. 2. *G. contractum* sp. no. 3. *G. musei* Danysz. After Pouchet (1887, pl. 10, fig. 6). 4. *G. rubricauda* sp. nov. 5. *G. fusus* Schütt. After Schütt (1895, pl. 24, fig. 79). 6. *G. scopulosum* sp. nov. 7. *G. flavum* sp. nov. 8. *G. rotundatum* Klebs. After Klebs (1912, p. 392, fig. 5). 9. *G. uberrimum* (Allman) Kofoid and Swezy. After Penard (1891, pl. 5, fig. 8). 10. *G. bogoriense* Klebs. After Klebs (1912, fig. 7). 11. *G. violescens* sp. nov. 12. *G. minor* Lebour. After Lebour (1917*b*, fig. 8). 13. *G. marinum* Saville-Kent. After Saville-Kent (1880–82, pl. 25, fig. 60). 14. *G. biciliatum* Ohno. After Ohno (1911, pl. 1, fig. 4). 15. *G. ovulum* sp. nov. 16. *G. palustre* Schilling. After Schilling (1891*a*, pl. 10, fig. 11). 17. *G. lineopunicum* sp. nov. 18. *G. mirabile* Penard. After Penard (1891, pl. 5, fig. 1). 19. *G. fuscum* (Ehrenberg) Stein. After Ehrenberg (1838, pl. 22, fig. 15). 20. *G. filum* Lebour. After Lebour (1917*b*, fig. 9). 21. *G. ravenescens* sp. nov. 22. *G. grammaticum* Pouchet. After Pouchet (1887, pl. 10, fig. 8). 23. *G. varians* Maskell. After Maskell (1887, pl. 1, fig. 9). 24. *G. viride* Penard. After Penard (1891, pl. 4, fig. 11). 25. *G. aeruginosum* Schilling. After Schilling (1891*a*, pl. 10, fig. 10). 26. *G. paradoxum* Schilling. After Schilling (1891*a*, pl. 10, fig. 13). 27. *G. conicum* Lebour. After Lebour (1917*b*, fig. 4). 28. *G. cinctum* sp. nov. 29. *G. vorticella* Stein. After Stein (1883, pl. 3, fig. 1). 30. *G. fulgens* nom. sp. nov. After Lebour (1917*b*, fig. 3). 31. *G. doma* sp. nov. 32. *G. dissimile* sp. nov. 33. *G. incisum* sp. nov. 34. *G. carinatum* Schilling. After Schilling (1891*a*, pl. 10, fig. 12). 35. *G. pseudonoctiluca* Pouchet. After Pouchet (1885*a*, pl. 4, fig. 34). × 500.

In the subgenus *Pachydinium* (figs. Z, AA), containing the most highly differentiated species of the genus, striae, furrows and ridges are found, as well as a pellicle devoid of such surface markings. Most of the species with the latter condition have an uneven surface contour, due to the well developed alveolar layer, the component parts of which are rounded outwardly, as in *G. pachydermatum* (fig. AA, 5). Many of the species exhibit a marked radial arrangement of the metaplasmic products. Two species, *G. abbreviatum* (pl. 6, fig. 63) and *G. situla* (pl. 1, fig. 12), have striae in addition to this noticeable unevenness of surface. *G. lira* has the surface marked by high ridges (fig. W, 1).

The genus *Gymnodinium* shows a range of coloring remarkable for its diversity and brilliancy. While nearly all the colors of the spectrum are represented, the predominating one is yellow, with its various shades and tones. The coloring may be confined to chromatophores, as in many of the species in the subgenus *Gymnodinium sensu strictu,* or diffused throughout the cytoplasm, as in most of the other species. In *G. lineopunicum* (pl. 6, fig. 65) the pomegranate purple pigment is aggregated into oblong masses and a coarse network, which constantly changes in outline and position. In *G. violescens* (pl. 6, fig. 69) the amaranth purple pigment is collected into small disks thickly scattered through the peripheral layer. The pigment is very frequently collected at the apices, particularly when aggregated into masses. In some species, as *G. pachydermatum* and *G. dogieli* (pl. 3, figs. 32, 34), the color is largely confined to the peripheral layers of cytoplasm, and is usually densest near the apices or at the girdle. In other species it is diffused uniformly throughout the body, as in *G. situla* (pl. 1, fig. 12).

In the more generalized species in the subgenus *Gymnodinium sensu strictu* the predominating colors are yellow, yellow ochre, and green. This group is made up largely of those species possessing chromatophores. The six species showing the greatest variation from this color scheme, to wit, *G. violescens* (pl. 6, fig. 69), *G. lineopunicum* (pl. 6, fig. 65), *G. sulcatum* (pl. 8, fig. 83), *G. rubricauda* (pl. 8, fig. 88), and *G. contractum* (pl. 5, fig. 52), while exhibiting colors which are not found elsewhere in the genus, with two exceptions, do not present a greater complexity of structure beyond that inherent in the color itself, as in *G. lineopunicum.* Two species, *G. rubrum* (pl. 8, fig. 86) and *G. lineatum* (pl. 1, fig. 2) in the subgenus *Lineadinium,* have the same rose red color found in *G. sulcatum.* These species show a slight advance, however, as one at least. *G. rubrum,* evidently forms one of the connecting links between *Gymnodinium* and *Gyrodinium.* The predominating colors in the subgenus *Lineadinium* are yellow and green, with blue in *G. translucens* (pl. 2, fig. 17) and neutral tints in *G. multilineatum* (pl. 5, fig. 59). In the subgenus *Pachydinium* the colors are diversified, yet here, too, yellow orange is conspicuous. The most highly differentiated species, *G. pachydermatum, G. dogieli,* and *G. amphora* (pl. 3), have this color, yet *G. abbreviatum* (pl. 6, fig. 63), with also a high degree of specialization, is pink in color. *Gymnodinium puniceum,* with

its onion-skin pink, is totally unlike the colors found elsewhere in the Gymnodiniidae (pl. 3, fig. 51). *Gymnodinium coeruleum* is one of the few species showing a clear blue color. Other species sometimes show a faint bluish tinge, as occasionally in *G. gracile* and *G. canus*. It is noteworthy here that those species having colored pigment aggregated into clumps have the shades of red, purple, and violet found in *Gyrodinium* and in some of the most highly specialized forms in *Cochlodinium, Pouchetia,* and *Erythropsis*. These colors are found in the most generalized group of the genus *Gymnodinium*. On the other hand the rich orange yellow found in the most highly specialized members of that genus is entirely lacking in *Erythropsis* and *Pouchetia* and nearly so in *Cochlodinium*. The line of development, in so far as determined by the color, leads onward from the more generalized species of the genus and not from its most highly specialized ones.

The species of this genus are in part holophytic and in part holozoic. The predominant type of nutrition in the more generalized subgenus *Gymnodinium* is holophytic, the majority of species in that group possessing chromatophores, yellow, yellow ochre, and green in color. In some of these forms, however, the possibility of holozoic nutrition, even when chromatophores are present, is not altogether excluded, as shown by the presence of foreign bodies in the cytoplasm, as in *G. agile* (fig. Y, 9), *G. herbaceum* (fig. Y, 17), *G. ravenescens* (fig. X, 21), and *G. flavum* (fig. X, 7). This condition is similar to that in *Amphidinium steini* (Stein, 1883, pl. 17, figs. 14–16) and *A. scissum* (pl. 2, fig. 22). In the species *G. fulgens* (Lebour's (1917*b*) *G. pseudonoctiluca,* our fig. X, 30) several large bodies are present, but no intimation is given as to their nature. The cytoplasm of *G. herbaceum* particularly is filled with the accumulated products of metabolism in the form of oil droplets and green, blue, and grey vacuoles.

In the next two subgenera, *Lineadinium* and *Pachydinium,* nutrition is probably largely, if not entirely, holozoic. In the first named group indisputable evidence of this is found in one species only, *G. heterostriatum*. The individuals of this species observed under the microscope proved to be insatiable cannibals. The actual process of ingestion was not observed, but very few specimens were noted which did not contain large food masses. In many cases these were recognizable as species of Gymnodinioidae (pl. 5, fig. 56). Their ejection from a posterior vent in the body was often seen. In many of the other species the cytoplasm usually contains oil droplets, vacuoles and refractive bodies, the accumulations of the products of metabolism suggestive of holozoic nutrition. These are especially striking in the subgenus *Pachydinium*. The body here is frequently filled with large food masses, as in *G. puniceum* and *G. sphaericum*. The sulcus in the midregion of the body probably functions as the mouth, and the posterior part of the body, particularly the sulcal notch, as the vent for ejecting foreign particles and fecal masses.

Cyst formation is common in *Gymnodinium,* and the cyst generally takes the form of a very thin, hyaline membrane. A second or even third membrane

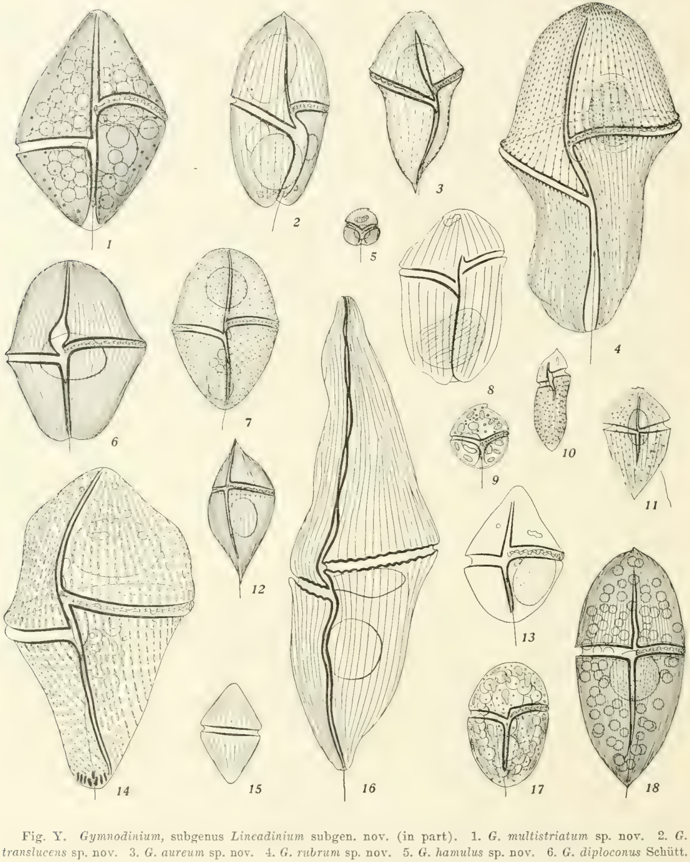


Fig. Y. *Gymnodinium,* subgenus *Lineadinium* subgen. nov. (in part). 1. *G. multistriatum* sp. nov. 2. *G. translucens* sp. nov. 3. *G. aureum* sp. nov. 4. *G. rubrum* sp. nov. 5. *G. hamulus* sp. nov. 6. *G. diploconus* Schütt. 7. *G. heterostriatum* nom. sp. nov. 8. *G. achromaticum* Lebour. After Lebour (1917*b*, fig. 5). 9. *G. agile* sp. nov. 10. *G. vestifici* Schütt. After Schütt (1895, pl. 25, fig. 85). 11. *G. helveticum* Penard. After Penard (1891, pl. 5, fig. 10). 12. *G. attenuatum* sp. nov. 13. *G. auratum* sp. nov. 14. *G. lineatum* sp. nov. 15. *G. rhomboides* Schütt. After Schütt (1895, pl. 21, fig. 63). 16. *G. cucumis* Schütt. After Schütt (1895, pl. 24, fig. 64). 17. *G. herbaceum* Kofoid. 18. *G. multilineatum* sp. nov. × 500.

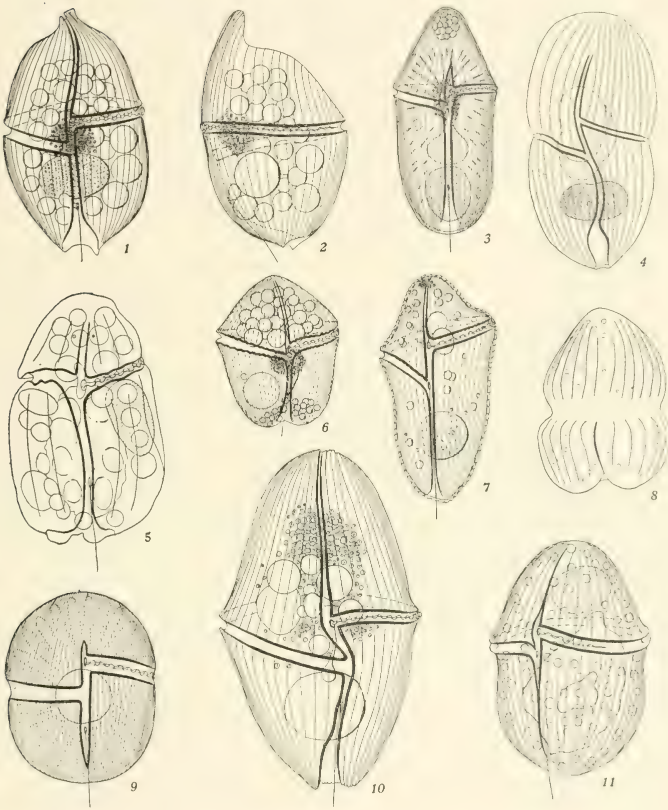


Fig. Z. *Gymnodinium,* subgenus *Pachydinium* subgen. nov. 1, 2. *G. canus* sp. nov. 1. Ventral view. 2. Lateral view. 3. *G. gracile* Bergh. 4. *G. coeruleum* Dogiel. After Dogiel (1906, pl. 2, fig. 47). 5. *G. puniceum* sp. nov. 6. *G. situla* sp. nov. 7. *G. abbreviatum* sp. nov. 8. *G. wilczeki* Pouchet. After Pouchet (1894, pl. 22, fig. 1). 9. *G. radiatum* sp. nov. 10. *G. costatum* sp. nov 11. *G. lira* sp. nov. × 500.

may be formed in succession, the outer usually large, as a result of distention, the inner following the contour of the body very closely (pl. 5, fig. 53). This inner membrane forms as a thin pellicle on the outer surface of the body and is expanded by incoming fluid.

DISTRIBUTION.—The occurrence of *Gymnodinium* has been recorded mainly from waters of temperate latitudes. Two species only, *G. wilczeki* and *G. pseudonoctiluca*, were found by Pouchet in scant numbers in the Arctic Ocean near Spitzbergen, July 31, 1892. One marine species has been recorded from the tropics, *G. fusus*, by Karsten (1907) in the Indian Ocean at 2° 58′ 5 N, 46° 50′ S E. Klebs (1912) found three fresh-water species near Buitenzorg, Java, *G. aeruginosum, G. borgoriense,* and *G. varians.*

Of the remainder, twenty are fresh-water forms. Of these the greater number of species have been found in Switzerland as the result of the work of the Swiss naturalist Penard. The following species are recorded from Lake Geneva: *G. helveticum, G. viride,* and *G. rufescens* (*G. uberrimum*) by Penard (1891), *G. palustre* by Guyer (1910); and from other waters in Switzerland, *G. carinatum, G. fuscum,* and *G. paradoxum* by Schilling (1891*a*), and *G. aeruginosum* by Amberg (1900). The lakes and ponds in Germany have also proved a fertile field, particularly the Lake Plön region. The species recorded here are: *G. paradoxum* by Lemmermann (1903*a*); *G. helveticum* and *G. tenuissimum* by Lauterborn (1894, 1910); *G. palustre* by Schilling (1891*a*); *G. fuscum* by Apstein (1896) and others; *G. zachariasi* by Zacharias (1899); *G. rotundatum* by Klebs (1912); and *G. aeruginosum* by Marsson (1901). Allman (1854, 1855) reported *G. uberrimum* (as *Peridinium uberrima*) from Dublin, Ireland. West and West (1909*a*) found *G. paradoxum* in both the English and Scottish lakes and *G. zachariasi* in the Irish lakes. From Austria-Hungary Entz (1910) has recorded *G. zachariasi* and Stein (1878) *G. vorticella* and *G. aeruginosum.* The latter species has also been recorded from the Finnish lakes, with *G. fuscum*, by Levander (1894*b*, 1900). *Gymnodinium fuscum* was noted in the Zealand and Jutland lakes in Denmark by Wesenberg-Lund (1904) and in Brazil by Cunha (1913), who also recorded *G. viride* from the same place. Butschinsky (1897) records *G. aeruginosum* from Odessa, Russia, and Bolochonzew (1903) *G. palustre* from the Volga River. A single record comes from New Zealand of *G. varians* by Maskell (1887) and one of *G. biciliatum* from Japan by Ohno (1911). The species *G. musei* was noted at Paris, France, by Pouchet (1887).

Of these fresh-water species *G. fuscum* and *G. aeruginosum* are the most widely distributed. Unfortunately the location of the discovery of *G. fuscum* in Brazil has not been given by Cunha (1913), so that no deductions can be made in regard to its temperature relations.

Of the twenty marine species the larger number come from the Mediterranean and the Atlantic. These are *G. cucumis, G. diploconus, G. fusus, G. gleba, G. rhomboides,* and *G. vestifica,* described by Schütt (1895). Unfortu-

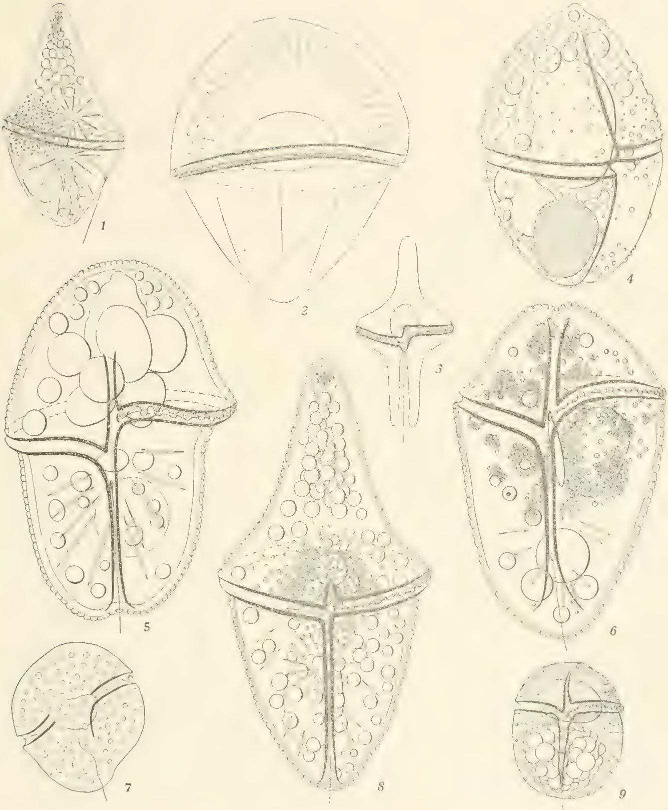


Fig AA. *Gymnodinium*, subgenus *Pachydinium* subgen. nov. Magnification 500, except where otherwise stated. 1. *G. dogieli* sp. nov. × 350. Lateral view. 2. *G. bifurcatum* sp. nov. Lateral view. 3. *G. bifurcatum* sp. nov. × 333. Ventral view. 4. *G. gleba* Schütt. After Schütt (1895, pl. 25, fig. 86). 5. *G. pachydermatum* sp. nov. 6. *G. amphora* sp. nov. 7. *G. tenuissimum* Lauterborn. After Lauterborn (1894, pl. 2, fig. 26). 8. *G. dogieli* sp. nov. 9. *G. sphaericum* Calkins.

nately he neglected entirely to give the source of his material, but it is stated by him (*in litt.*) to be in the greater part from the Gulf of Naples. Pouchet (1887) described *G. grammaticum* from the Atlantic off the coast of France; Calkins (1902) found *G. sphaericum* (*G. gracile* var. *sphaerica*) off Woods Hole, Mass., and Wright (1907) figures *G. gracile* from Nova Scotian waters. From the waters of the North Sea, the Skager Rack and Cattegat, are recorded: *G. pyrocystis* by Jörgensen (1912); *G. rhomboides* by Paulsen (1907); *G. vestifici* by Lohmann (1908) and Ostenfeld (1913), and *G. gracile* by Ostenfeld (1913). From the Mediterranean, particularly the Bay of Naples, come *G. heterostriatum*, *G. lunula*, and *G. coeruleum*, recorded by Dogiel (1906), and *G. grammaticum*, recorded by Schröder (1900). *G. gracile* is recorded by Bergh from the Baltic Sea, as is also *G. vestifici* by Lohmann (1908). Of the remaining records Lebour (1917*b*) gives *G. minor*, *G. fulgens* (*G. pseudonoctiluca*), *G. achromaticum*, *G. conicum* (*G. viridis*), *G. rhomboides*, and *G. filum* from Plymouth Sound, England, and Pouchet (1894) describes *G. wilczeki* from the Arctic Ocean. Saville-Kent has described *G. marinum* from an infusion of hay and sea water at St. Heliers, Isle of Jersey.

Thus far no species have been described from the Pacific Ocean. To these twenty marine species we herewith add one new species, *G. herbaceum* Kofoid MSS, from the Bay of Naples, and thirty-five new species from the Pacific Ocean off the coast of California near San Diego, as follows: *G. abbreviatum*, *G. agile*, *G. amphora*, *G. attenuatum*, *G. auratum*, *G. aureum*, *G. bicorne*, *G. bifurcatum*, *G. canus*, *G. cinctum*, *G. costatum*, *G. contractum*, *G. dissimile*, *G. dogieli*. *G. doma*, *G. flavum*, *G. hamulus*, *G. incisum*, *G. lira*, *G. lineatum*, *G. lineopunicum*, *G. multilineatum*, *G. multistriatum*, *G. ovulum*, *G. pachydermatum*, *G. puniceum*, *G. radiatum*, *G. ravenescens*, *G. rubricauda*, *G. rubrum*, *G. scopulosum*, *G. situla*, *G. sulcatum*, *G. translucens*, and *G. violescens*. In addition we give new records for the occurrence of the following seven species in the Pacific at San Diego: *G. diploconus* Schütt, *G. gleba* Schütt, *G. gracile* Bergh, *G. heterostriatum* nom. sp. nov. (= *G. obtusum* Dogiel), *G. lunula* Schütt, *G. rhomboides* Schütt, *G. sphaericum* Calkins (= *G. gracile* var. *sphaerica* Calkins).

Prior to the establishment of *Gymnodinium* by Stein in 1878 the imperfection of our knowledge of the dinoflagellates in general, the lack of information as to the relations of the armored and unarmored forms, the slight data on encystment and the misinterpretation of the transverse flagellum as a row of cilia, all conspired to prevent the recognition of this genus and scatter its representatives in other genera, often ill founded. Thus the first species belonging to it, *G. fuscum*, was described by Ehrenberg (1834) as *Peridinium fuscum*. Later (1840) this same indefatigable explorer described very briefly as *Peridinium monas* a species which Saville-Kent (1880–82) doubtfully refers to his *Gymnodinium marinum*. The greatest synonymical confusion was created by Diesing's two attempts (1850, 1866) to reorganize the classification of helminths, which at that time included many of the imperfectly known microscopical forms of life. In his Systema *Helminthum* (1850) he included in his

new genus *Heteraulacus* Ehrenberg's *Peridinium fuscum* and *P. monas* and Schmarda's (1846) *P. adriaticum*. He changed this generic name in his later *Revision der Prothelminthen* (1866) to *Heteroaulax* and added thereto Schmarda's (1854) *Peridinium inerme*. Allman's (1854) species *uberrima* was placed by him in *Peridinium*, but was later made the type of *Melodinium* by Saville-Kent (1880–82), but it clearly belongs to *Gymnodinium*, established in 1878 by Stein.

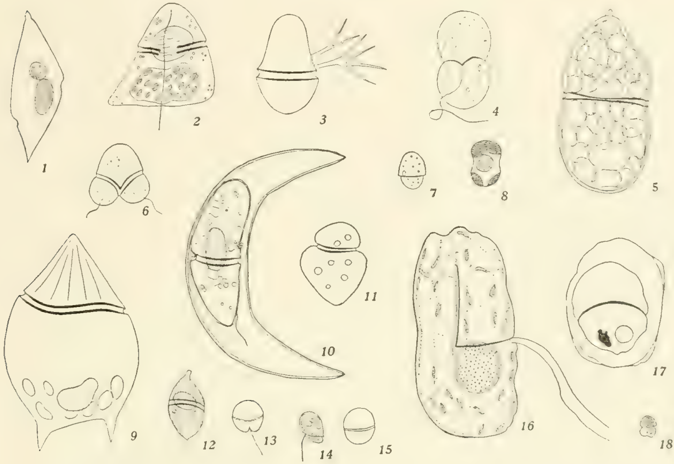


Fig. BB. *Gymnodinium*. 1. *G. lohmanni* (Paulsen). After Lohmann (1908, pl. 17, fig. 26). 2. *G. triangularis* Lebour. After Lebour (1917*b*, fig. 7). 3. *G. zachariasi* (Zach.) Lemm. After Zacharias (1899, fig. 4). 4. *G. lachmanni* Saville-Kent. After Saville-Kent (1880–82, pl. 25, fig. 59). 5. *G. lohmanni* Paulsen. After Lohmann (1908, pl. 17, fig. 25). 6. *G. lachmanni* Saville-Kent. After Saville-Kent (1880–82, pl. 25, fig. 58). 7. *G. monadicum* (Perty). After Perty (1852, pl. 7, fig. 15). 8. *G. simplex* (Lohm.). After Lohmann (1908, pl. 17, fig. 17). 9. *G. bicaudatum* Pavillard. After Pavillard (1905, pl. 3, fig. 5). 10. *G. bicorne* sp. nov. 11. *G. roseolum* (Schm.). After Schmarda (1854, pl. 1, fig. 9). 12. *G. lohmanni* Paulsen. After Lohmann (1908, pl. 17, fig. 28). 13. *G. tintinnicola* Lohmann. After Lohmann (1908, pl. 17, fig. 6). 14. *G. corpusculum* (Perty). After Perty (1852, pl. 7, fig. 14). 15. *G. inerme* (Schm.). After Schmarda (1854, pl. 1, fig. 8). 16. *G. rete* Schütt. After Schütt (1895, pl. 21, fig. 63). 17. *G. gracile* v. *exiguum* Pouchet. After Pouchet (1883, pl. 21, fig. 40). 18. *G. punctatum* Pouchet. After Pouchet (1887, pl. 10, fig. 7). × 500.

## Historical Discussion

This genus was established by Stein (1878) for two species described by Ehrenberg (1834, 1838) as *Peridinium fuscum* and *P. pulvisculus.* He considered this the basic type for the more complex Peridiniidae. Later (1883) he changed *Gymnodinium pulvisculus* (Ehr.) to *Glenodinium pulvisculus.* He also (1883) described *Gymnodinium aeruginosum* and *G. vorticella* and transferred to the genus Schmarda's *Glenodinium roseolum* as *Gymnodinium roseolum.* His use of the species designation *G. pulvisculus* has proved a source of some confusion in later literature. Klebs (1883) records, without figuring, a form from fresh water as *G. pulvisculus* with a note that he is not certain of its identity with Stein's species, overlooking the fact that Stein had changed that species to *Glenodinium.* Pouchet (1885*a*) later gives the name *G. pulvisculus* to a *Gymnodinium*-like organism parasitic on *Appendicularia.* Lemmermann (1899) reserves the name *G. pulvisculus* for Kleb's form and gives to Pouchet's parasitic organism the name *G. poucheti.* Chatton (1906) notices the close relation of Pouchet's species with his newly created genus *Blastodinium*, changing its name to *Oodinium poucheti.* As a parasitic genus with a complicated life cycle it does not belong with *Gymnodinium* as that genus is at present constituted, and we therefore reject it, placing it with the Blastodiniidae. With it and for the same reason we reject *G. parasiticum,* parasitic on copepods, and *G. affinis* from *Gymnodinium.*

Protozoologists following Stein placed in this genus forms representing *Gymnodinium*, *Gyrodinium*, *Cochlodinium*, and *Pouchetia* as here constituted. Bergh (1881*b*) added to the genus *G. gracile* and also *G. spirale*, later changed by Schütt (1896) to *Spirodinium spirale* and by us to *Gyrodinium spirale.* The same year Penard (1881) described *G. helveticum, G. mirabile, G. mirabile* var. *rufescens,* changed by Lemmermann (1900) to *G. rufescens* and *G. viride* (= *G. uberrinum* Allman). Saville-Kent (1880–82) added *G. marinum* and *Danysz* (1886), *G. musci.* Pouchet described the following species, to which we add our present allocation of them:

*Gymnodinium archimedes,* (1883) = *Cochlodinium archimedes* Lemmermann (1899).

*G. spirale* var. *striatum,* (1883) = *Gyrodinium fissum* Kofoid and Swezy.

*G. spirale* var. *cornutum,* (1885*a*) = *Spirodinium cornutum* (Pouchet) Lemmermann (1899) = *Cochlodinium cornutum* (Pouchet) Kofoid and Swezy.

*G. teredo* (1885*a*) = *Torodinium teredo* (Kofoid and Swezy).

*G. crassum,* (1885*b*) = *Spirodinium crassum* (Pouchet) Lemmermann (1899) = *Gyrodinium crassum,* Kofoid and Swezy.

*G. polyphemus,* (1885*b*) = *Pouchetia polyphemus* (Pouchet) Kofoid and Swezy.

*G. helix* (1887) = *Cochlodinium helix* (Pouchet) Lemmermann (1899).

*G. polyphemus* var. *nigrum,* (1887) = *Pouchetia nigra* (Pouchet) Lemmermann; (1899) = *Protopsis nigra* (Pouchet) Kofoid and Swezy.

*G. pulvisculus* = *G. poucheti,* Lemmermann (1899) = *Oodinium poucheti* (Lemmermann) Chatton (1912).

*G. polyphemus* var. *roseum*, (1887) = *Pouchetia rosea* (Pouchet) emend. Kofoid and Swezy.
*G. gracile* var. *exiguum*, (1883) = *incertae sedis*, not *G. gracile*.
*G. punctatum* var. *grammaticum* (1887) = *G. grammaticum* (Pouchet) Kofoid and Swezy.
*G. pseudonoctiluca* (1885*a*).
*G. punctatum*, (1887).
*G. wilczeki*, (1894).

Bütschli (1885) added no new species to the genus, but includes in it Pouchet's *G. archimedes* and Bergh's *G. spirale*. Schilling (1891*a*) added to the fresh-water species the following: *G. carinatum*; *G. hyalinum* = *Spirodinium hyalinum* (Schilling) Lemmermann (1900) = *Gyrodinium hyalinum* (Schilling) Kofoid and Swezy; *G. paradoxum*, and *G. pusillum* = *Gyrodinium pusillum* (Pouchet) Kofoid and Swezy.

Levander (1894) added *G. fissum*, which was changed by Lemmermann (1900) to *Spirodinium fissum* and by us to *Gyrodinium fissum*. Schütt in his first treatment of the subject (1895) included the species *Spirodinium* (= *Gyrodinium*) and *Cochlodinium* in Gymnodinium, but the following year (1896) he established these two genera, making *Gymnodinium spirale* Bergh the type for *Spirodinium* and *Gymnodinium strangulatum* (Schütt) the type for *Cochlodinium* by monospecific citation. He failed, however, to sort out the representatives of these two new genera from the remaining twenty-two new species which he had earlier described as *Gymnodinium*. These are given in the following list with their present allocation, if changed:

*Gymnodinium spirale* var. *acuta* = *Spirodinium spirale* var. *acutum* (Schütt) Lemmermann (1899) = *Gyrodinium acutum* (Schütt) Kofoid and Swezy.
*G. constrictum* = *Cochlodinium constrictum* (Schütt) Lemmermann (1899).
*G. contortum* = *Gyrodinium contortum* (Schütt) Kofoid and Swezy.
*G. cornutum* = *Spirodinium schuettii* Lemmermann (1899) = *Gyrodinium cornutum* (Schütt) Kofoid and Swezy.
*G. cucumis*.
*G. diploconus*.
*G. fusus*.
*G. geminatum* = *Cochlodinium geminatum* (Schütt) Lemmermann (1899).
*G. gleba*.
*G. lunula*.
*G. spirale* var. *mitra* = *Spirodinium spirale* var. *mitra* (Schütt) Lemmermann (1899) = *Gyrodinium mitra* (Schütt) Kofoid and Swezy.
*G. spirale* var. *obtusa* = *Spirodinium spirale* var. *obtusum* (Schütt) Lemmermann (1899) = *Gyrodinium obtusum* (Schütt) Kofoid and Swezy.
*G. opimum* = *Gyrodinium contortum* Kofoid and Swezy.
*G. ovum* = *Gyrodinium ovum* (Schütt) Kofoid and Swezy.
*G. parvulum* = *Gyrodinium parvulum* (Schütt) Kofoid and Swezy.
*G. spirale* var. *pepo* = *Spirodinium spirale* var. *pepo* (Schütt) Lemmermann (1899) = *Gyrodinium pepo* (Schütt) Kofoid and Swezy.
*G. spirale* var. *pinguis* = *Spirodinium spirale* var. *pinque* (Schütt) Lemmermann (1899) = *Gyrodinium pinque* (Schütt) Kofoid and Swezy.

*G. pirum* = *Cochlodinium pirum* (Schütt) Lemmermann (1899).
*G. rete* = *incertae sedis,* probably near *Hemidinium.*
*G. rhomboides.*
*G. vestifici.*
*G. viride* = *Gyrodinium foliaceum* Kofoid and Swezy.

Maskell (1887) described *G. varians*, Lauterborn (1894) followed with *G. tenuissimum*, and Lemmermann (1900) added *G. zachariasi* (Zachariasi). In 1902 Calkins added the species *G. gracile* var. *sphaerica*, changed by us to *G. sphaericum.* Dogiel (1906) described *G. coeruleum, G. affine, G. parasiticum, G. roseum* (= *Chytriodinium roseum,* Chatton, 1912), and *G. spirale* var. *obtusum*, changed by us to *G. heterostriatum*, Küster (1908) added *G. fucorum*, an imperfectly characterized *Gyrodinium.* Ohno added *G. biciliatum* in 1911. In 1912 Klebs described *G. bogoriense*, *G. minimum*, which we consider identical with *G. varians* Maskell, and *G. rotundatum.* In the same year Jörgensen added to the list *G. pyrocystis.* Lebour (1917*b*) was the last investigator to add to this list with the following:

*G. achromaticum, G. filum, G. minor, G. pseudonoctiluca* Pouchet = *G. fulgens* Kofoid and Swezy.
*G. viridis* = *G. conicum* Kofoid and Swezy.
*G. triangularis,* a doubtful species.

The genus *Protodinium* (Lohmann, 1908) presents the characteristics of the genus *Gymnodinium* without distinct generic features of its own, hence we place it with *Gymnodinium*, and the single species *Protodinium simplex* Lohmann as *Gymnodinium simplex.*

The following is a summary of the species which we consider valid in the foregoing list, giving (1) the fresh-water species and (2) the marine forms:

(1) *Gymnodinium aeruginosum* Stein, *G. biciliatum* Ohno, *G. bogoriense* Klebs, *G. carinatum* Schilling, *G. fuscum* (Ehrenberg) Stein, *G. helveticum* Penard, *G. mirabile* Penard, *G. musci* Danysz, *G. palustre* Schilling, *G. paradoxum* Schilling, *G. rotundatum* Kelbs, *G. roseolum* (Schmarda) Stein, *G. tenuissimum* Lauterborn, *G. uberrimum* (Allman) Kofoid and Swezy, *G. varians* Maskell, *G. viride* Penard, *G. vorticella* Stein, *G. zachariasi* Lemmermann.

(2) *Gymnodinium achromaticum* Lebour, *G. coeruleum* Dogiel, *G. cucumis* Schütt, *G. diploconus* Schütt, *G. filum* Lebour, *G. fusus* Schütt, *G. gleba*, *G. gracile* Bergh, *G. grammaticum* (Pouchet), *G. lunula* Schütt, *G. marinum* Saville-Kent, *G. minor* Lebour, *G. pseudonoctiluca* Pouchet, *G. punctatum* Pouchet, *G. pyrocystis* Jörgensen, *G. rhomboides* Schütt, *G. simplex* (Lohmann). *G. sphaericum* Calkins, *G. vestifici* Schütt, *G. wilczeki* Pouchet.

In addition to these forty-one valid species above enumerated we consider that the following must be placed in the list of *incertae sedis* for lack of sufficient data:

*G. affine* Dogiel (1906).
*G. corpusculum* (Perty) Saville-Kent (1880–82) (= *Peridinium corpusculum* Perty and *Proaulax corpusculum* (Perty) Diesing.
*G. gracile* var. *exiguum* Pouchet (1883).
*G. glaciale* Danysz (1886).
*G. inerme* (Perty) Saville-Kent (1880–82) (= *Peridinium inerme* Schmarda 1854 and *Heteraulax inermis* (Schmarda) Diesing (1866) as a synonym of *G. monadicum*).
*G. lachmanni*, Saville-Kent (1880–82) (= *Peridinium* sp. Claparède and Lachmann).
*G. lohmanni* Paulsen (1908) (= *G. roseum*, Lohmann, 1908), pl. 17, fig. 25. His figures 26–28 of the same plate are evidently *Gyrodinium*.
*G. monadicum* (Perty) Saville-Kent (1880–82) (= *Peridinium monadicum* Perty, 1852).
*G. monas* (Ehrenberg) Saville-Kent (1880–82), cited by Kent as possibly the same as *G. marinum*. Indeterminable.
*G. paradoxum* var. *major* (Lemm.) West and West (1906). May be *G. paradoxum*.
*G. rete* Schütt (1895). May be *Hemidinium*.
*G. simplex* (Lohmann) 1908 (= *Protodinium simplex*).
*G. tintinnicola* Lohmann (1908).
*G. triangularis* Lebour (1917*b*).

The following are placed in the list of *nomina nuda:*

*G. asymmetricum* Massart (1901).
*G. cruciatum* Massart (1901).
*G. polyphemus* var. *magna* Dogiel (1906).
*G. minutissimum* Massart (1901).
*G. vorax* Massart (1901).

The following species, included at some time heretofore in *Gymnodinium*, have been transferred by others or are by us here transferred to other genera:

*G. spirale* var. *acuta* Schütt (1895) to *Gyrodinium* nom. gen. nov. by us in this paper as *G. acutum*.
*G. archimedes* Pouchet (1883) to *Cochlodinium* by Lemmermann (1899).
*G. bicaudatum* Pavillard (1905) to *Heterodinium bicaudatum* (Pavillard) by us in this paper.
*G. constrictum* Schütt (1895) to *Cochlodinium* by Lemmermann (1899).
*G. contortum* Schütt (1895) to *Gyrodinium* nom. gen. nov. by us in this paper.
*G. cornutum* Schütt (1895) to *Gyrodinium* nom. gen. nov. by us in this paper.
*G. spirale* var. *cornutum* Pouchet (1885*a*) to *Gyrodinium* nom. gen. nov. by us as *G. cornutum* in this paper.
*G. crassum* Pouchet (1885*a*) to *Gyrodinium* nom. gen. nov. by us in this paper.
*G. fissum* Levander (1894) to *Gyrodinium* nom. gen. nov. by us in this paper.
*G. fucorum* Küster (1908) to *Gyrodinium* nom. gen. nov. by us in this paper.
*G. geminatum* Schütt (1895) to *Cochlodinium* by Lemmermann (1899).
*G. helix* Pouchet (1887) to *Cochlodinium* by Lemmermann (1899).
*G. hyalinum* Schilling (1891*a*) to *Gyrodinium* nom. gen. nov. by us in this paper.
*G. spirale* var. *mitra* Schütt (1895) to *Gyrodinium* nom. gen. nov. by us in this paper as *G. mitra*.

*G. nasutum* (Stein) Levander (1900) to *Hemidinium* by us in this paper.
*G. noctiluca* Pouchet (1885*a*) to *Noctiluca miliaris* by us in this paper.
*G. polyphemus* var. *nigrum* Pouchet (1887) to *Protopsis* nom. gen. nov. by us in this paper as *Protopsis nigrum*.
*G. spirale* var. *obtusa* Schütt (1895) to *Gyrodinium* nom. gen. nov. by us in this paper as *G. obtusum*.
*G. opimum* Schütt (1895) to *Gyrodinium* nom. gen. nov. by us in this paper.
*G. ovatum* Gourret (1883) to *Gyrodinium* nom. gen. nov. by us in this paper.
*G. ovum* Schütt (1895) to *Gyrodinium* nom. gen. nov. by us in this paper.
*G. parasiticum* Dogiel (1906) to *Oodinium parasiticum* (Dogiel) Kofoid and Swezy.
*G. parvulum* Schütt (1895) to *Gyrodinium* nom. gen. nov. by us in this paper.
*G. spirale* var. *pepo* Schütt (1895) to *Gyrodinium* nom. gen. nov. as *G. pepo* by us in this paper.
*G. spirale* var. *pinguis* Schütt (1895) to *Gyrodinium* nom. gen. nov. as *G. pinguis* by us in this paper.
*G. pirum* Schütt (1895) to *Cochlodinium* by Lemmermann (1899).
*G. polyphemus* Pouchet (1887) to *Pouchetia polyphemus* (Pouchet) emend. Kofoid and Swezy.
*G. poucheti* Lemmermann (1899) (= *Gymnodinium pulvisculus* Pouchet, 1885*a*) to *Oodinium poucheti* (Lemmermann) by Chatton (1912).
*G. pulvisculus* Pouchet (1885*a*) to *Oodinium poucheti* (Lemm.) by Chatton (1912).
*G. pulvisculus* (Ehrenberg, 1830) Stein (1878) to *Glenodinium pulvisculus* (Ehrbg.) by Stein (1883).
*G. pusillum* Schilling (1891*a*) to *Gyrodinium* nom. gen. nov. by us in this paper.
*G. roseum* Dogiel (1906) to *Chytriodinium roseum* (Dogiel) by Chatton (1912).
*G. polyphemus* var. *roseum* Pouchet to *Pouchetia rosea* (Pouchet) Kofoid and Swezy emend.
*G. spirale* Bergh (1881*b*) to *Gyrodinium* nom. gen. nov. by us in this paper.
*G. spirale* vars. *C, D,* Pouchet (1883) to *Gyrodinium* nom. gen. nov. by us in this paper as *G.*
*G. strangulatum* Schütt (1895) to *Cochlodinium* by Lemmermann (1899).
*G. spirale* var. *striatum* Pouchet (1883) to *Gyrodinium* nom. gen. nov. by us in this paper as *G. striatum*.
*G. teredo* Pouchet (1885*a*) to *Torodinium* gen. nov. by us in this paper.
*G. viride* Schütt (1895) to *Gyrodinium* nom. gen. nov. by us in this paper.

## Subgenera of **Gymnodinium**

### Subgenus 1. **Gymnodinium** subgen. nov.

Medium to small sized species, with or without chromatophores, surface free from markings or if present few and scattered. The type species is *G. fuscum* (Ehrenberg). This subgenus includes besides the type: *G. aeruginosum* Stein, *G. agile* sp. nov., *G. auratum* sp. nov., *G. biciliatum* Ohno, *G. bicorne* sp. nov., *G. bogoriense* Klebs, *G. carinatum* Schilling, *G. cinctum* sp. nov., *G. conicum* nom. sp. nov., *G. contractum* sp. nov., *G. dissimile* sp. nov., *G. doma* sp. nov., *G. filum* Lebour, *G. flavum* sp. nov., *G. fulgens* nom. sp. nov., *G. fusus* Schütt, *G. grammaticum* (Pouchet), *G. herbaceum* Kofoid, *G. incisum* sp. nov., *G.*

*lineopunicum* sp. nov., *G. lunula* Schütt, *G. marinum* Saville-Kent, *G. minor* Lebour, *G. mirable* Penard, *G. musei* Danysz, *G. ovulum* sp. nov., *G. palustre* Schilling, *G. paradoxum* Schilling, *G. pseudonoctiluca* Pouchet, *G. punctatum* Pouchet, *G. pyrocystis* Jörgensen, *G. ravenescens* sp. nov., *G. roseolum* (Schmarda), *G. rotundatum* Klebs, *G. rubricauda* sp. nov., *G. scopulosum* sp. nov., *G. simplex* (Lohmann), *G. sulcatum* sp. nov., *G. tintinnicola* Lohmann, *G. uberrimum* (Allman), *G. varians* Maskell, *G. viride* Penard, *G. violescens* sp. nov., *G. vorticella* Stein, and *G. zachariasi* (Zacharias).

### SUBGENUS 2. **Lineadinium** subgen. nov.

Periplast thin, surface striate with parallel linear striae on epicone and hypocone. Generally of large size.

Type species is *G. heterostriatum* nom. sp. nov. It includes also the following species: *G. achromaticum* Lebour, *G. attenuatum* sp. nov., *G. aureum* sp. nov., *G. cucumis* Schütt, *G. diploconus* Schütt, *G. hamulus* sp. nov., *G. helveticum* Penard, *G. lineatum* sp. nov., *G. multilineatum* sp. nov., *G. multistriatum* sp. nov., *G. rhomboides* Schütt, *G. rubrum* sp. nov., *G. translucens* sp. nov., *G. vestifici* Schütt.

### SUBGENUS 3. **Pachydinium** subgen. nov.

Pellicle distinctly thickened, usually conspicuous as a wide zone around the body, with the outer alveolar layer making the surface bossed or mammilate. Surface marked by striae or ridges, or smooth. The type species is *G. pachydermatum* sp. nov. It includes besides the type: *G. abbreviatum* sp. nov., *G. amphora* sp. nov., *G. bifurcatum* sp. nov., *G. canus* sp. nov., *G. coeruleum* Dogiel, *G. costatum* sp. nov., *G. dogieli* sp. nov., *G. gleba* Schütt, *G. gracile* Bergh, *G. lira* sp. nov., *G. puniceum* sp. nov., *G. radiatum* sp. nov., *G. sphaericum* Calkins, *G. situla* sp. nov., *G. tenuissimum* Lauterborn, and *G. wilczeki* Pouchet.

### SPECIES OF UNCERTAIN STATUS IN **Gymnodinium**

Owing to the fact that a free, non-thecate phase of brief duration may occur in the life history of the Peridinioidae, it is possible to mistake them for the true Gymnodinioidea. The characteristics which distinguish such phases are little known. These phases are wont to be more active than the thecate phase of the species and to be less frequently observed and less completely described. The activity of the unarmored forms in general tends to introduce into literature records of species based on partial observations which do not reveal the relationships or establish the status of the form described.

The following species described in the genus *Gymnodinium* are in our opinion so imperfectly characterized as to render their allocation tentative and to require fuller description before their status therein and their relationships

can be determined: *Gymnodinium bicaudatum* Pavillard (1905), *G. corpusculum* (Perty, 1852) Saville-Kent (1880–82), *G. gracile* var. *exiguum* Pouchet (1883), *G. inerme* (Schmarda) Saville-Kent, *G. lachmanni* Saville-Kent (1880-82), *G. lohmanni* (Lohmann, 1908), *G. monadicum* (Perty, 1852) Saville-Kent (1880-82), *G. punctatum* Pouchet (1887), *G. rete* Schütt (1895), *G. simplex* Lohmann (1908), *G. tintinnicola* Lohmann (1908), *G. triangularis* Lebour (1917*b*), *G. monas* (Ehrenberg, 1840), Saville-Kent (1880–82).

In the following discussion of the species of the genus *Gymnodinium* an alphabetical arrangement of both the valid and doubtful species has been preserved solely as a matter of convenience:

## Key to the Species of **Gymnodinium**

| | |
|---|---|
| 1. Periplast thin, without striae, or if present limited and few | (subgenus **Gymnodinium**) 2 |
| 1. Periplast thin, with striae | (subgenus **Lineadinium**) 58 |
| 1. Periplast thickened, surface striate or smooth | (subgenus **Pachydinium**) 42 |
| 2. Striae or furrows on epicone or hypocone, not on both | 3 |
| 2. No striae | 5 |
| 3. Surface with furrows on epicone only | **contractum** sp. nov. |
| 3. Surface markings in hypocone only | 4 |
| 4. About 8 furrows on hypocone | **sulcatum** sp. nov. |
| 4. Hypocone with 18–20 striae | **herbaceum** Kofoid MSS. |
| 5. Chromatophores present | 6 |
| 5. No chromatophores | 22 |
| 6. In fresh water, chromatophores green | 7 |
| 6. Chromatophores yellow or nearly so | 9 |
| 7. Girdle postmedian, chromatophores scattered | **musei** Danysz |
| 7. Girdle submedian, disklike chromatophores crowding the periphery | **aeruginosum** Stein |
| 7. Girdle median, rod-shaped chromatophores radially arranged | 8 |
| 8. Length, $35\mu$ | **viride** Penard |
| 8. Length, $17\mu$ | **varians** Maskell |
| 9. Pseudopodia extended from sulcus | **zachariasi** Lemm. |
| 9. Pseudopodia not known to occur | 10 |
| 10. Marine species | 11 |
| 10. Fresh-water species | |
| 11. Large species, length over $100\mu$ | 12 |
| 11. Length less than $100\mu$ | 13 |
| 12. Body biconical, girdle medium length, $122\mu$, 2.1 transdiameters | **fusus** Schütt |
| 12. Body with conical epicone, girdle premedian, length $100\mu$, 2.3 transdiameters | **fulgens** nom. sp. nov. |
| 13. Girdle not displaced | 14 |
| 13. Girdle displaced at least its own width | 16 |

14. With apical point deflected to the left, body spheroidal ........ **agile** sp. nov.
14. Apical point, if present, not deflected ........ 15
15. Length 1.5 transdiameters, girdle feebly marked ........ **simplex** (Lohmann)
15. Length 1.2 transdiameters, girdle evident ........ **grammaticum** (Pouchet)
16. Sulcus not extended far on epicone, length less than $40\mu$ ........ 17
16. Sulcus extending nearly to apex, length over $50\mu$ ........ 18
17. Epicone and hypocone subequal, girdle not constricting ........ **flavum** sp. nov.
17. Epicone much smaller than hypocone, girdle deeply constricting ........ **cinctum** sp. nov.
18. Epicone hemispherical, dark ochraceous ........ **conicum** nom. sp. nov.
18. Epicone conical, greenish yellow ........ **ravenescens** sp. nov.
19. Length over $75\mu$ ........ 20
19. Length less than $50\mu$ ........ 21
20. Sulcus extending short distance on epicone, girdle slightly displaced ........ **mirabile** Penard
20. Sulcus confined to hypocone, girdle not displaced ........ **fuscum** (Ehrenberg)
21. Length about 1 to 1.1 transdiameters ........ 22
21. Length about 1.3 to 1.5 transdiameters ........ 24
22. Girdle slightly displaced, length $45\mu$, yellowish brown ........ **uberrimum** (Allman)
22. Girdle not displaced ........ 23
23. Length $44\mu$, over 1.5 transdiameters, yellowish brown ........ **palustre** Schilling
23. Length $40\mu$, 1.3 transdiameters, dark brown ........ **paradoxum** Schilling
23. Length $34\mu$, 1.3 transdiameters, yellowish ........ **rotundatum** Klebs
24. Length $40\mu$, 1.5 transdiameters ........ **carinatum** Schilling
24. Length $22–23\mu$ ........ 25
25. Sulcus extends short distance on epicone ........ **biciliatum** Ohno
25. No sulcus on epicone ........ **bogoriense** Klebs
26. Cytoplasm colored ........ 27
26. Cytoplasm colorless ........ 37
27. Fresh-water, cytoplasm pink, girdle premedian ........ **roseolum** (Schmarda)
27. Marine habitat ........ 28
28. Pigment masses present ........ 29
28. No pigment masses present ........ 30
29. Pigment pomegranate purple, peripheral ........ **lineopunicum** sp. nov.
29. Pigment pansy violet, in disks or scattered ........ **violescens** sp. nov.
29. Pigment rose red, diffused, and in spherules ........ **rubricauda** sp. nov.
30. Length over $100\mu$, girdle premedian, temporary tentacle present ........ **pseudonoctiluca** Pouchet
30. Length less than $100\mu$ ........ 31
31. Girdle premedian, epicone low hemispherical, sulcus short ........ **doma** sp. nov.
31. Girdle not premedian, sulcus extends from apex to antapex ........ 32

32. Girdle postmedian, greyish green, 48$\mu$ ........ **dissimile** sp. nov.
32. Girdle median or submedian ........ 33
33. Length equaling transdiameter, sulcal notch present ........ **incisum** sp. nov.
33. Length more than 1.2 transdiameters ........ 34
34. Length over 2.5 transdiameters, cyst arcuate ........ **bicorne** sp. nov.
34. Length less than two transdiameters ........ 35
35. Length 1.8 transdiameters, 47$\mu$, girdle displaced 0.3 transdiameter.... **scopulosum** sp. nov.
35. Length less than 1.5 transdiameter, girdle slightly displaced ........ 36
36. Spherical and lunate cysts common, free form 22$\mu$, 1.22 transdiameters...... **lunula** Schütt
36. Cysts unknown, length 62$\mu$, 1.4 transdiameters ........ **auratum** sp. nov.
37. Fresh-water species, girdle postmedian, length less than 30$\mu$ ........ **vorticella** Stein
37. Marine species ........ 38
38. Large species, length 200$\mu$ ........ **pyrocystis** Jörgensen
38. Less than 100$\mu$ in length ........ 39
39. Girdle postmedian, body broadly ellipsoidal ........ **minor** Lebour
39. Girdle premedian or nearly so ........ 40
40. Body slender biconical ........ **filum** Lebour
40. Body spheroidal ........ **ovulum** sp. nov.
40. Body ovoidal, dorsoventrally compressed ........ **marinum** Saville-Kent
41. Body with thickened periplast, striate or non-striate, **Pachydinium** subgen. nov. ........ 42
41. Periplast thin, striate, **Lineadinium** subgen. nov. ........ 58
42. Large species, over 100$\mu$ in length ........ 43
42. Less than 100$\mu$ in length ........ 54
43. Surface striate or furrowed ........ 44
43. Surface not marked with striae or furrows ........ 50
44. Striae subequal on epicone and hypocone ........ 45
44. Striae more numerous on hypocone ........ 47
45. Girdle premedian, striae broken, surface rough, color pink ........ **abbreviatum** sp. nov.
45. Girdle submedian ........ 46
46. Epicone contracted obliquely on dorsal surface, greenish ........ **canus** sp. nov.
46. Epicone symmetrical, pink ........ **costatum** sp. nov.
47. Color blue, girdle median ........ **coeruleum** Dogiel
47. Color not markedly blue, girdle premedian ........ 48
48. Length over 2 transdiameters at girdle, epicone conical ........ **gracile** Bergh
48. Length not over 2 transdiameters ........ 49
49. Epicone 0.35 total length, color onion-skin pink ........ **puniceum** sp. nov.
49. Epicone 0.40 total length, color greyish green ........ **lira** sp. nov.
50. Surface roughened by alveolar layer, ectoplasm distinct ........ 51
50. Surface smooth, ectoplasm not distinct ........ 53

51. Epicone concave conical, girdle submedian, scarcely displaced ..................**dogieli** sp. nov.
51. Epicone convex, subhemispherical, girdle slightly displaced .................................................. 52
52. Epicone about 0.35 total length ....................................................................**amphora** sp. nov.
52. Epicone nearly 0.5 total length ...................................................**pachydermatum** sp. nov.
53. Hypocone bifurcated about 0.8 its length, color pink ..........................**bifurcatum** sp. nov.
53. Hypocone not bifurcated, color greenish grey ...............................................**gleba** Schütt
54. Surface striate or furrowed ............................................................................................ 55
54. Surface not striate or furrowed ...................................................................................... 57
55. Coarsely striate, girdle scarcely displaced, submedian ..............................**wilczeki** Pouchet
55. Finely striate, girdle premedian, at least proximally ..................................................... 56
56. Girdle distinctly premedian, scarcely displaced, epicone low conical ..........**situla** sp. nov.
56. Girdle premedian proximally, displaced 2 furrow widths, epicone hemispherical .............. ...................................................................................................................**radiatum** sp. nov.
57. Body dorsoventrally compressed, fresh-water ................................**tenuissimum** Lauterborn
57. Body not compressed, marine .........................................................................**sphaericum** Calkins
58. Length 3 or more transdiameters ........................................................................................ 59
58. Length less than 3 transdiameters ...................................................................................... 60
59. Length $210\mu$, girdle submedian ...............................................................**cucumis** Schütt
59. Length $47\mu$, girdle far anterior ...............................................................**vestifici** Schütt
60. Pigment present ............................................................................................................... 61
60. Pigment not present ........................................................................................................... 62
61. Girdle premedian, striae on hypocone more numerous than on epicone, rose red .............. .........................................................................................................................**rubrum** sp. nov.
61. Girdle submedian, striae equal in number on epicone and hypocone, rose red .................... ......................................................................................................................**lineatum** sp. nov.
62. Length less than $20\mu$, apical point deflected to left .....................................**hamulus** sp. nov.
62. Length over $20\mu$, apical point, if present, not strongly deflected ......................................... 63
63. Red or pink ........................................................................................................................ 64
63. Not red or pink .................................................................................................................. 65
64. Fresh-water habitat, striae equal on epicone and hypocone ..................**helveticum** Penard
64. Marine habitat, striae more numerous on hypocone ................**heterostriatum** nom. sp. nov.
65. Girdle not displaced, body biconical, yellow ............................................**diploconus** Schütt
65. Girdle displaced ................................................................................................................ 66
66. Length more than 2 transdiameters ................................................................................... 67
66. Length less than 2 transdiameters ..................................................................................... 68
67. Body biconical, apices tapering, length $65\mu$ ...........................................**attenuatum** sp. nov.
67. Body elongate ellipsoidal, length $100\mu$ .............................................**multilineatum** sp. nov.
68. Colorless, translucent, or bluish ....................................................................................... 69
68. Color yellow ....................................................................................................................... 71

69. Body symmetrically biconical, length $46\mu$ .......... **rhomboides** Schütt
69. Body ellipsoidal, length over $50\mu$ .......... 70
70. Girdle median, minute apical point present .......... **translucens** sp. nov.
70. Girdle premedian, apex broadly rounded .......... **achromaticum** Lebour
71. Hypocone rotund below girdle, color ochraceous yellow, striae more numerous on hypocone .......... **multistratum** sp. nov.
71. Hypocone contracted below girdle, color, strontium yellow, striae equal on epicone and hypocone .......... **aureum** sp. nov.

## **Gymnodinium abbreviatum** sp. nov.

Plate 6, figure 63; text figure Z, 7

Diagnosis.—A medium sized species with elongate ovoidal body, its length 1.94 transdiameters; hypocone elongated; girdle premedian with displacement of 0.26 transdiameter; sulcus extending from apex to antapex; differentiated ectoplasm; surface striate and mammillated; color, hydrangea pink. Length, $97\mu$. Pacific off La Jolla, California, July, August.

Description.—The body is long, elongate, asymmetrically ovoidal, widest anteriorly at the girdle, rounded at the apices and circular in cross-section, its length 1.94 transdiameters at the widest part. The hypocone greatly exceeds the epicone in size, its length being greater than the extreme length of the latter by 0.27 of itself. The epicone is subconical (80°) in shape, flaring widely towards the girdle, with a blunt, rounded, somewhat eccentrically placed apex inclined dextrally. It has a length on the left and right sides of 0.3 and 0.47 respectively of the total length of the body. The hypocone is long, flaring slightly anteriorly, tapering posteriorly, with asymmetrically rounded antapex slightly notched by the sulcus, the left side being somewhat longer than the right.

The girdle is premedian in position, its proximal and distal ends joining the sulcus at distances from the apex of about 0.3 and 0.47 respectively of the total length of the body. About 0.75 of its course around the body is in a transverse direction and the remainder is deflected posteriorly, its distal end meeting the girdle at an angle of about 45° with the main axis of the body, with a displacement of 0.26 transdiameter. The furrow has a width of 0.06 transdiameter, and is rather shallow with overhanging borders, the lips of which present a crinkled outline caused by the unevenness in the surface of the body. The sulcus extends from the apex to the antapex, beginning at the left of the apex and terminating at the right of the antapex. It forms a deep trough, narrowed above and below its junctions with the girdle and enlarging considerably between them. Its borders are smooth throughout. The anterior flagellar pore opens at the anterior junction and the posterior pore at the posterior junction of the girdle and sulcus.

The nucleus is a large, ellipsoidal body located in the posterior half of the hypocone. Its chromatin contents are arranged in fine moniliform strands. Its major and minor axes are about 0.48 and 0.44 transdiameters in length respectively.

Club-shaped pusules may be present at either or both pores. The cytoplasm is finely granular and is frequently filled with large salmon pink vacuoles. Besides these, oil globules of varying sizes and minute refractive granules are generally abundant. Near the anterior flagellar pore a large olive green food mass was present in the individual figured. The general color of the organism is hydrangea pink diffused throughout the cytoplasm. The ectoplasm forms a thick, distinct layer and is composed of large bosses with the outer surface rounded, giving the outline

of the body a distinctly wavy appearance (fig. Z, 7). This layer is about 1$\mu$ in thickness. On the surface of the body are striae of broken lines, linearly arranged and spaced at about 3$\mu$ near the girdle, twenty-three across the ventral face.

DIMENSIONS.—Length, 97–115$\mu$; transdiameter, 50–75$\mu$; axes of nucleus, 25–36$\mu$ and 22–28$\mu$.

OCCURRENCE.—The individual figured was taken July 9, 1917, 4 miles off La Jolla, California, with a No. 25 silk net in a haul from 80 meters to the surface and in a surface temperature of 19°2 C. On July 11 another individual was observed in a surface haul made at the same place, with the same apparatus. It was seen again on August 13, 0.75 mile off La Jolla in a haul from 83 meters to the surface.

COMPARISONS.—Lebour (1917*b*) describes a form to which she gives the name *G. achromaticum,* which is somewhat similar to our species, and yet presents striking differences. The general shape and proportions differ only in a slight degree (fig. Y, 8). The most striking difference is in the lack of a differentiated ectoplasm in *G. achromaticum*, which in *G. abbreviatum* gives the characteristic appearance to the surface. This species shows the same differentiated ectoplasm found in *G. dogieli* sp. nov., *G. pachydermatum* sp. nov., and *G. amphora* sp. nov. (figs. AA, 1, 5, 6), and, like them, it belongs to the subgenus *Pachydinium.* In its color it stands alone in *Gymnodinium,* and in displacement of girdle exceeds that in the species above named.

## **Gymnodinium achromaticum** Lebour

Text figure Y, 8

*Gymnodinium achromaticum* Lebour (1917*b*), p. 190, fig. 5.

DIAGNOSIS.—A medium sized species with ellipsoidal body, its length 1.62 transdiameters; girdle premedian, displaced about twice its own width; sulcus extending from girdle to antapex; surface coarsely striate; colorless. Length, 78$\mu$. Plymouth Sound, England, July.

DESCRIPTION.—The body is asymmetrically and broadly ellipsoidal in ventral view, with broadly rounded apices, ovoidal in lateral view, narrowing posteriorly, its length 1.62 transdiameters at the widest part. The narrowing of the dorsoventral diameter occurs only in the posterior part of the hypocone. The epicone is much smaller than the hypocone, being exceeded in length by 0.24 of the length of the hypocone. Its shape is that of a broad, flat cone, about 90° in lateral view, 120° in ventral view, with blunt apex excentrically placed sinistro-ventrad. It has a length on the left and right sides of about 0.29 and 0.48 respectively of the total length of the body. The hypocone is long with subparallel sides in ventral view, tapering posteriorly in lateral view. The antapex is broad and truncate, marked ventrad by the sulcal notch.

The girdle is premedian, joining the proximal end of the sulcus at a distance from the apex of about 0.29 of the total length of the body. It sweeps around the body in a descending left spiral course, its distal end joining the sulcus 0.48 of the total length of the body from the apex, and is displaced about twice its own width. The furrow is wide, about 0.08 transdiameter, and is deeply impressed, with overhanging sides. The sulcus apparently extends upon the epicone for a short distance and posteriorly to the antapex in a slightly sinuous line. The flagella and pores are not figured by Lebour (1917*b*).

The nucleus is ellipsoidal and is situated in the posterior part of the body. It is filled with chromatin strands which traverse its longer axis. Its major and minor axes are about 0.62 and 0.43 transdiameters respectively in length.

The surface is sparsely covered with longitudinal striae, about ten across the ventral face, apparently equal in number on the epicone and hypocone. The organism is stated by Lebour (1917*b*) to be perfectly colorless and transparent.

Dimensions.—Length, 78μ; transdiameter, 48μ; axes of nucleus, 32 and 21μ.

Occurrence.—A single individual was seen by Lebour (1917*b*) July, 1915, in a haul made in Plymouth Sound, England.

Comparisons.—It falls within the subgenus *Lineadinium* by reason of its thin periplast and striate surface in the group including also *G. puniceum* sp. nov. (fig. Z, 5) and *G. wilczeki* Pouchet, species with rotund body and sparse striae. Its girdle displacement separates it from *G. puniceum* and its small epicone from *G. wilczeki.* This form resembles *G. abbreviatum* somewhat closely, yet differs from it in its lack of a thick ectoplasm, in its fewer striae, and in its slightly different proportions.

### **Gymnodinium adriaticum** (Schmarda) Kofoid and Swezy

*Peridinium adriaticum* Schmarda (1846), pp. 19, 36, 62, pl. 2, figs. 1, 1–5; (1847), p. 12.
*Heteraulacus adriaticum,* Diesing (1850), p. 100.
*Heteroaulax adriatica,* Diesing (1866), p. 95.
*Peridinium adriaticum,* Stein (1878), p. 72.
*P. adriaticum,* Maggi (1880*a*), p. 14; (1880*b*), pp. 314, 326.
*P. adriaticum,* Imhof (1886), p. 101.
Not *Peridinium adriaticum* Broch (1910), pp. 179, 191–193, fig. 8.

Diagnosis.—Body stout, ellipsoidal with hemispherical apices. its length 1.5 transdiameters, widest at the girdle; epicone and hypocone subequal; girdle equatorial without displacement or overlap; sulcus straight, slight sulcal notch; ochraceous; length, 30–54μ. Adriatic Sea.

Description.—The body is very symmetrically ellipsoidal, transverse and dorsoventral diameters equal; its length 1.43–1.54 transdiameters, widest at the girdle, which is equatorial in location. The epicone and hypocone are subequal, each a little more than a hemisphere by elongation near the girdle, apex rounded, antapex with broad shallow sulcal notch. The girdle is transverse, without deflection or overlap, and the sulcus is confined to the hypocone. The transverse flagellum encircles the body, while the longitudinal one projects 0.8 of the length of the body behind the postmargin, but the origin of the flagella is not shown.

The nucleus is subcentral, to the left and posterior to the girdle. It is spheroidal, 0.23 transdiameter in diameter. Cytoplasm with numerous small spherules. Color ochraceous.

Dimensions.—Length, 35–54μ; transdiameter, 30–35μ, rarely 21–45μ.

Occurrence.—Described by Schmarda (1846) as very abundant in salt pools of St. Servola on the northern coast of the Adriatic Sea, and as rare in ponds filled by sea water from the inner Venetian lagoons, but abundant in a similar pool at the Forts of the Lido at Venice. It was not found by Imhof (1886), who examined the plankton in Venetian lagoons, and, though cited in literature, has not been reported since its discovery by Schmarda.

SYNONYMY.—Described by Schmarda (1846) as *Peridinium adriaticum* and transferred by Diesing (1850) to his genus *Heteraulacus* and later (1886) to *Heteroaulax*.

In 1910 Broch described from the Adriatic a true thecate *Peridinium* which he named *adriaticum* sp. nov. This name is preoccupied by Schmarda's (1846) *P. adriaticum*. We therefore propose the name *Peridinium brochi* nom. sp. nov. for Broch's species.

COMPARISONS.—This species is close to *G. fuscum* (Ehrenberg, 1834), but differs from it as figured in smaller size, stouter body and rounded antapex, as well as in being a marine instead of a fresh-water form. It is also rather near *G. marinum* Saville-Kent (1880–82), but is less constricted and has a relatively larger epicone.

## **Gymnodinium aeruginosum** Stein

Text figure X, 25

*Gymnodinium aeruginosum* Stein (1883), pl. 2, figs. 19–22.
*G. aeruginosum,* Bütschli (1885), p. 986.
*G. aeruginosum,* Levander (1894*a*), p. 43; (1894*b*), p. 210; (1901), p. 6.
*G. aeruginosum,* Schilling (1891), p. 276, pl. 10, fig. 10; (1913), p. 19, fig. 18.
*G. aeruginosum,* Schütt (1895), pp. 9, 58.
*G. aeruginosum,* Entz (1896), p. 22; (1902), p. 120; (1910), p. 157.
*G. aeruginosum,* Butschinsky (1897), p. 195.
*G. aeruginosum,* Mez (1898), p. 216.
*G. aeruginosum,* Lemmermann (1899), p. 126; (1900), p. 116; (1901), p. 358; (1902), p. 260; (1905), p. 163; (1906), p. 420; (1910), pp. 613–623, figs. 12–14.
*G. aeruginosum,* Schönichen and Kalberlah (1900), p. 231; (1909), p. 252.
*G. aeruginosum,* Amberg (1900), p. 83.
*G. aeruginosum,* Marsson (1901), p. 103.
*G. aeruginosum,* Ruttner (1906), pp. 9, 16.
*G. aeruginosum,* Paulsen (1908), p. 100, fig. 138.
*G. aeruginosum,* Lauterborn (1910), p. 452.
*G. aeruginosum,* Kolkwitz (1911), pp. 347, 371.
*G. aeruginosum,* Klebs (1912), p. 391.
*G. aeruginosum,* Zenker (1912), p. 27.
*G. aeruginosum,* West (1916), pp. 52, 75.

DIAGNOSIS.—A minute species with ellipsoidal, dorsoventrally flattened body, its length 1.57 transdiameters; girdle slightly postmedian, without displacement; sulcus extending from the middle of the epicone to the antapex; color blue green. Length, 33$\mu$. Fresh water in Austria, Finland, Russia, Germany, and Switzerland.

DESCRIPTION.—The body is ellipsoidal, widest near the middle, with broad apices, its length 1.57 transdiameters, its dorsoventral diameter 0.3 of its transdiameter. The epicone is slightly larger than the hypocone, having a length 0.17 greater. It is broadly dome-shaped in ventral view with broad apex. Its length is 0.5 of the total length of the body. Its sides are rounded and the antapex is truncate or excavated by the sulcal notch.

The girdle is slightly postmedian, its distance from the apex being 0.5 of the total length of the body. It forms a complete circle around the body. The furrow is about 0.1 transdiameter in width and deeply impressed with overhanging borders. The sulcus begins midway between the girdle and the apex and extends posteriorly in a straight line to or near the antapex. The transverse and longitudinal flagella both arise near together at the junction of the girdle and sulcus.

The nucleus is a spherical body near the apex. Its diameter is about 0.2 transdiameter of the body. Numerous blue green chromatophores fill the peripheral zone of the cytoplasm and give their color to the organism.

DIMENSIONS.—Length, 33–34μ; transdiameter, 21–22μ; diameter of sulcus, 5μ.

OCCURRENCE.—Figured by Stein (1883) from fresh-water ponds near Chodau, Austria. Other occurrences reported are as follows: Levander (1894*a*) from several lakes in Finland and (1894*b*) near Helsingfors, Finland; Butschinsky (1897) at Odessa, Russia; Amberg (1900) at Zurich, Switzerland; Marsson (1901) near Berlin, Germany; Ruttner (1906) near Prag, Austria; Kolkwitz (1911) eastern Russia and western Germany; Entz (1896) in Hungary; Zenker (1912) near Hildesheim, Germany; and Klebs (1912) near Buitenzorg, Java.

Klebs's (1912) record of the occurrence of this species in the tropical waters of Java may be held as tentative, since he gives no figures or description. The change from the cool temperate regions of Finland and Germany to the tropical waters of Java, about 15° C, might be expected to result in specific differences.

COMPARISONS.—This species is closely related to *G. palustre* and *G. viride* in size, form, and habitat, and is one of a small group of fresh-water species, most of them possessing brownish or greenish chromatophores and of an elongated, subovoidal form, about 1.5 transdiameters in length. This species differs from all others of the group in having bluish green, elliptical, disklike chromatophores.

## **Gymnodinium agile** sp. nov.

Plate 3, figure 31; text figure Y, 9

DIAGNOSIS.—A minute species with body rounded disklike, its length 1.07 transdiameters, with sinistral apical point; girdle median, without displacement; sulcus extending from girdle to antapex; colorless, with orange green chromatophores. Length, 28μ. Pacific off La Jolla, California, July, August.

DESCRIPTION.—The body is rounded in ventral view, flattened dorsoventrally, with broad apices, its length 1.07 transdiameters at the widest part, its dorsoventral diameter 0.4 of its transdiameter. The epicone and hypocone are subequal. The epicone is subhemispherical with the apex displaced to the left as a minute, pointed, finger-like projection bending downward towards the surface of the body. The length of the epicone is about 0.5 of the total length of the body. The hypocone is symmetrically hemispherical in ventral view, with the antapex occasionally notched by the distal end of the sulcus.

The girdle is equatorial in position and is without displacement, forming a complete circle around the body. The furrow is broad, about 0.08 transdiameter, and deep with smooth,

overhanging borders. The anterior flagellar pore opens at its junction with the sulcus, the posterior pore about 1.5 widths of the girdle posterior to the anterior one. The transverse flagellum traverses about 0.3 of the length of the girdle.

The sulcus extends from the girdle to the antapex as a wide, rather deep trough, which widens at both ends. In some individuals the distal extremity notches the antapex.

The nucleus is ellipsoidal and anteriorly placed. Chromatin strands could not be detected in its structure. Its major and minor axes are about 0.5 and 0.34 transdiameter in length respectively.

A sacklike, bright coral-red pusule opens into each flagellar pore. The cytoplasm is clear and colorless. Minute refractive bodies are numerous in the epicone and absent in the hypocone, in which part a single large amyloid, or food body, is present. In both hypocone and epicone are a few flat, ellipsoidal, orange green chromatophores, comparatively large, and located in the periphery. A distinct, double-contoured pellicle surrounds the body. Nutrition is probably holophytic.

Dimensions.—Length, 28$\mu$; transdiameter, 26$\mu$; dorsoventral diameter, 10$\mu$; major and minor axes of nucleus, 14$\mu$ and 19$\mu$ respectively.

Occurrence.—The individual figured was taken from the beach sand at La Jolla, California, July 3, 1917. Others were present in the same material and in the material examined at a later date. One individual was taken August 13, 0.75 of a mile off La Jolla, in a haul made from 80 meters to the surface.

This form was associated with *Amphidinium dentatum*, *A. corpulentum*, and *A. scissum*, all typical beach forms. It presents two of the characteristics of these species in its dorsoventrally flattened body and chromatophores.

Comparisons.—This species resembles *G. hamulus* in the possession of a sinistral apical point, but differs from it in its larger size, and absence of striae. The point is suggestive of the extension of the sulcus to the apex.

### **Gymnodinium amphora** sp. nov.

Plate 3, figure 26; text figure AA, 6

Diagnosis.—A large species with stout ovoidal body, its length 1.58 transdiameters; girdle premedian, displaced nearly twice its own width; sulcus extending from apex to antapex; color green yellow. Length, 151$\mu$. Pacific off La Jolla, California, August.

Description.—The body is large, ovoidal, nearly circular in cross-section, widest anteriorly at the girdle and tapering posteriorly, with broad apices, its length 1.58 transdiameters at the widest part. The hypocone greatly exceeds the epicone in size, being 0.45 of its own length longer than the epicone. The epicone forms an asymmetrical, broad, rounded, cap-shaped part of the body with a length on the left and right sides of 0.33 and 0.36 of the total length of the body respectively. It forms a cone of nearly 90°. The apex is broad and widely notched near the end of the sulcus. The hypocone is more symmetrical than the epicone, elongate, rounded conical (30°), with the antapex much narrower than the apex, but without sulcal notch.

The girdle is premedian in position and passes around the body in a slightly descending left spiral direction, with a displacement of about twice its own width. The furrow is wide, about 0.05 transdiameter, and deeply imbedded with overhanging, slightly undercut borders. The proximal and the distal ends join the sulcus at distances from the apex of respectively about

0.33 and 0.36 of the total length of the body. The sulcus begins at the apex and extends posteriorly in an almost straight line to near the antapex. It lies in a rather wide shallow trough with rounded sides which fade out in the apical regions. The anterior flagellar pore is slightly below the proximal junction of the girdle and sulcus. The posterior pore opens at about 0.58 of the distance between the anterior pore and the antapex.

The nucleus is spherical and located in the posterior third of the body. Its axis is about 0.27 transdiameter in length. A long sacklike pusule opens into the anterior flagellar pore. The cytoplasm is clear and finely granular, and filled with metabolic products, evidences of holozoic nutrition. In the central part of the body was a large, brownish food mass, obscured by a great mass of dark, refractive granules. Radiating out from this were long slender blue green rodlets, or radial canals. Smaller groups of granules filled the remaining central and anterior regions of the body, with a few small bodies, yellow ochre in color. In the antapical region were several large vacuoles filled with fluid, colored salmon pink like the pusule.

This species, like *G. dogieli,* has a distinct ectoplasmic region, composed of a thin layer surmounted by an alveolar layer, the outer portions of the alveoli being rounded and giving a roughened appearance to the surface of the body. This layer is appreciably thicker in the antapical region and is a striking feature of the body in a general view. The color of the organism is pale turquoise green shading to deep yellow on the right side of the hypocone, and slightly diffused throughout the cytoplasm, but with a greater concentration in the peripheral region. The surface exhibited no striae or other markings.

DIMENSIONS.—Length, 15$\mu$; transdiameter, 95$\mu$; axis of nucleus, 27$\mu$.

OCCURRENCE.—A single individual was taken on August 13, 1917, with a No. 25 silk net, 0.75 of a mile off La Jolla, California, in a haul from 80 meters to the surface and in a surface temperature of 21°9 C.

COMPARISONS.—This is one of the most highly differentiated species of *Gymnodinium*, as shown in its highly developed ectoplasm, and belongs with the subgenus *Pachydinium.* In its cytoplasmic structure, coloring, and size it stands very close to *G. dogieli* and *G. pachydermatum* (fig. AA, 8, 5), but differs greatly from them in its relative proportions and arrangement of girdle, having the shortest epitheca of the three and an anterior sulcal notch.

## **Gymnodinium attenuatum** sp. nov.

Text figure Y, 12

DIAGNOSIS.—A small species with ovate fusiform body, apices acute, compressed laterally, its length 2.24 transdiameters; girdle premedian, displaced less than its own width; sulcus extending from apex to near antapex; surface finely striate. Length, 65$\mu$. Pacific off La Jolla, California, June, July.

DESCRIPTION.—This is a small species with ovate body sharply pointed at both ends, and compressed laterally, its dorsoventral diameter equaling 1.17 transdiameters and its length 2.24 transdiameters. It is slightly asymmetrical with the ventral face having a greater convexity than the dorsal face. The epicone is nearly 0.5 shorter in length than the hypocone. The basal portion of the epicone is rotund, tapering anteriorly to a sharp, slender point. The apex is somewhat excentric, being thrown dorsad by the greater slope of the ventral face. Its length is about 0.3 of the total length of the body. The length of the hypocone is about 0.66 of the total length of the body. It is rounded anteriorly and tapers to a long, slender antapex.

The girdle is premedian in position, lying at about 0.3 of the total length of the body from the anterior end. It is narrow, shallow, and is displaced about half its own width. The anterior flagellar pore opens at its proximal junction with the sulcus, and the posterior pore midway between the girdle and antapex. The narrow, shallow sulcus invades the epicone to the apex. Below the girdle it extends posteriorly in a straight line, traversing about 0.7 of the distance from the girdle to the antapex.

The nucleus is elliptical in outline and centrally located with its major axis coinciding with the long axis of the body. Its chromatin contents could not be analyzed. Its major and minor axes are about 0.6 and 0.4 transdiameters in length respectively. The cytoplasm is clear with no large inclusions, but containing a number of oil globules and small, subspherical or irregular bodies superficially arranged. The surface is striate with equidistant, longitudinal striae about equal in number on both epicone and hypocone and about 20 at the girdle across the ventral face.

DIMENSIONS.—Length, 65–78$\mu$; transverse diameter, 29–38$\mu$; dorsoventral diameter, 34$\mu$; axes of nucleus, 17$\mu$ and 12$\mu$.

OCCURRENCE.—This species was first taken June 28, 1904, with a No. 20 net, in a haul 10 miles off La Jolla, California, from 120 meters to the surface. It was again found July 5, at the same distance offshore with the same apparatus, in a haul from a depth of 240 meters to the surface. On July 7 of the same year it was taken 11 miles off La Jolla in a surface haul.

COMPARISONS.—This species belongs to the subgenus *Lineadinium*, having the thin periplast and striate surface of that group, but is unique in its lateral compression and acute apices.

## **Gymnodinium auratum** sp. nov.

Plate 2, figure 20; text figure Y, 13

DIAGNOSIS.—A small species with ovoidal body, its length 1.44 transdiameters; epicone conical; girdle submedian, displaced slightly more than its own width; sulcus extending from apex to antapex; color old gold. Length, 62$\mu$. Pacific off La Jolla, California, August.

DESCRIPTION.—The body is broadly ovoidal, nearly circular in cross-section, broadly rounded posteriorly, conical anteriorly, its length 1.44 transdiameters at the girdle, the widest part. The length of the epicone and hypocone are subequal, but, owing to its rotundity, the hypocone exceeds the epicone in volume. The epicone is conical, about 70°, with a narrowly blunt apex. It has a length on the left and right sides of 0.43 and 0.54 of the total length of the body respectively. The hypocone is broadly rounded, with smooth antapex.

The girdle is submedian in position, its proximal and distal ends having a distance from the apex of 0.43 and 0.54 of the total length of the body respectively. It is wide, about 0.09 transdiameter, and deeply impressed with smooth lips. Its course around the body is that of a left descending shallow spiral, with its distal end displaced posteriorly slightly more than its own width. The sulcus is a shallow, narrow channel, its width about 0.3 of the width of the girdle. It extends from near the apex in a slightly sinuous course posteriorly to near the antapex. The anterior flagellar pore opens at the proximal junction of the girdle and sulcus, the posterior pore about two widths of the girdle posterior to the distal junction.

The nucleus is a large, ellipsoidal body found on the left side of the hypocone. It is filled with fine, moniliform, chromatin strands arranged parallel to its long axis, which is slightly oblique to the major axis of the body. Its major and minor axes are about 0.65 and 0.4 transdiameter in length respectively.

Small, club-shaped pusules open into each flagellar pore. The cytoplasm was unusually free from cell inclusions such as food bodies, vacuoles, etc. A small, irregular, dark green mass was found close beside the nucleus and farther anteriorly, another, slightly larger, of a neutral grey with a dark border. The cytoplasm is finely granular. The general color is old gold, quite deep posteriorly, shading to pale king's blue at the anterior end, with tones of light green and pearl grey through the girdle region. No striae or other markings could be detected on its surface. A thin hyaline cyst somewhat larger than the body, and closely following its contour, enclosed the organism.

DIMENSIONS.—Length, 62$\mu$; transdiameter, 43$\mu$; axes of nucleus, 28$\mu$ and 18$\mu$; length of cyst, 66$\mu$.

OCCURRENCE.—A single individual was observed August 20, 1917, from a haul made 0.75 of a mile off La Jolla, California, from 80 meters to the surface, and in a surface temperature of about 22° C.

COMPARISONS.—This species, because of the comparative simplicity of its organization and lack of surface markings, falls within the subgenus *Gymnodinium sensu strictu*. Its coloring suggests that of *G. amphora* (fig. AA, 6), but it differs greatly from that species in all other respects. In proportions it approaches rather distantly some of the biconical species of the subgenus *Lineadinium* (fig. Y), but lacks the striae which characterize that subgenus. It is nearest *G. violescens* sp. nov. (fig. X, 11), but is wholly different in color, has less displacement of girdle, and a fuller hypocone.

## **Gymnodinium aureum** sp. nov.

Plate 1, figure 5; text figure Y, 3

DIAGNOSIS.—A medium sized species with subovoidal body pointed posteriorly, its length 1.84 transdiameters; girdle premedian, displaced twice its own width; sulcus extending from near apex to antapex; surface striate; color strontium yellow. Length, 83$\mu$. Pacific off La Jolla, California, July.

DESCRIPTION.—The body is ovoidal, subtruncate-acuminate anteriorly, tapering to a slender point posteriorly, widest through the epicone, its length 1.84 transdiameters at the widest part and its dorsoventral diameter 0.85 transdiameter. The hypocone exceeds the epicone in size, being longer by 0.18 of its length. The epicone is conical in outline (70°). Its apex is truncate-acuminate with a median and two lateral elevations on the summit formed by two parasagittal creases across the apex. Its length is about 0.39 of the total length of the body, with the right side extending posteriorly in a slender point with a length of 0.47 of the total length. The hypocone is longer, less symmetrical than the epicone and is drawn out distally to a slender, pointed, ventrally flexed antapex. It has a width at the girdle equal to the width of the epicone, but is much narrower posteriorly.

The girdle is premedian in position, its proximal end meeting the sulcus at a distance from the apex of 0.39 of the total length of the body. It passes around the body in a nearly transverse direction for about 0.8 of its course, the latter part turning posteriorly so that the distal end is displaced about twice its own width. The furrow is wide, about 0.08 transdiameter, its distal end narrowed to less than half that width, and is deeply impressed with smooth, overhanging borders. The sulcus is somewhat variable in its length. It may invade the epicone a short distance only or may reach the neighborhood of the apex. The furrow is deep, varies

greatly in width, being usually wide at the girdle and at the posterior end of its course which is near the antapex. The anterior flagellar pore opens at the junction of the proximal end of the girdle and the sulcus and the posterior pore at their distal junction.

The nucleus is a large, ellipsoidal body located anterior to the equatorial plane. It is filled with fine, moniliform chromatin strands and shows a distinct double-contoured membrane surrounding it. Its major and minor axes are 0.46 and 0.52 transdiameter respectively. The cytoplasm is coarsely granular and was quite free from food bodies and vacuoles in the specimens examined. The surface is striate with longitudinal, equidistant blue-green striae composed of linear series of short broken lines. These are about the same number on both epicone and hypocone, approximately 16 across the ventral face. The color of the organism is a clear strontium yellow, diffused through the cytoplasm. It is probably holozoic in its nutrition.

DIMENSIONS.—Length, 83$\mu$; transdiameter, 45$\mu$; dorsoventral diameter, 39$\mu$; major and minor axes of nucleus, 13$\mu$ and 11$\mu$ respectively.

OCCURRENCE.—This was first observed July 11, 1906, in a haul with a No. 20 net, 2 miles off La Jolla, California, from 155 meters to the surface and in a surface temperature of 20°9 C. It was found July 9, 1917, in a haul with a No. 25 net, 4 miles offshore, from 80 meters to the surface and in a surface temperature of 19°8 C.

COMPARISONS.—This species bears a strong resemblance to *Gymnodinium helveticum* Penard. Penard's (1891) species, however, is a fresh-water form from Lake Geneva, Switzerland. Our species is probably the marine representative of the same group. Its size and proportions differ somewhat from those of *G. helveticum* and it has a greater displacement of the girdle. It belongs to the subgenus *Lineadinium*, but, aside from *G. helveticum*, there are no other species closely resembling it.

## **Gymnodinium bicaudatum** Pavillard

Text figure BB, 9

*Gymnodinium bicaudatum* Pavillard (1905), p. 47, pl. 3, fig. 5.

This organism was described by Pavillard (1905) from the Gulf of Lyons and seems to have suggestions in its symmetry of the characteristics of the thecate genus *Heterodinium* Kofoid. The data given are not sufficient to place it in *Gymnodinium*, or to define its specific characters. The two posterior projections are quite unlike anything in the unarmored dinoflagellates. It may be a thecate form recently escaped by exuviation of the skeleton and therefore temporarily non-thecate. The possibility of approaching division or of an antapical vent following ejection of food balls in an unarmored species is not precluded as an explanation of the bifurcated postmargin.

## **Gymnodinium biciliatum** Ohno

Text figure X, 14

*Gymnodinium biciliatum* Ohno (1911), pp. 77–91, pl. 1, figs. 1–37.

Diagnosis.—A minute species with broadly ellipsoidal body, its length 1.31 transdiameters; girdle without displacement; sulcus short on epicone, extending to near the antapex on hypocone; color yellow brown. Length, 22$\mu$. Fresh-water ponds in the Botanical Gardens at the Imperial University at Tokyo, Japan.

Description.—The body is broadly ellipsoidal with broad rounded apices, and its length is 1.31 transdiameters at the widest part. The hypocone exceeds the epicone in size, its length being greater by 0.2. The epicone has a length of about 0.4 of the total length of the body. The hypocone is subhemispherical posteriorly, with broad apex.

The girdle is premedian in position, its distance from the apex being 0.4 of the total length of the body. The furrow is wide, 0.09 transdiameter, and deeply impressed, with high rounded borders. The sulcus is a short shallow trough, its length about twice the width of the girdle. The longitudinal and transverse flagella arise in close proximity to each other at the junction of girdle and sulcus. Two longitudinal flagella are described and figured by Ohno (1911), hence the specific name.

The nucleus is not figured by him, but it evidently lies in the dark mass near the center of the body. Numerous oil droplets are contained within the cytoplasm. The color is yellow brown. Chromatophores appear to be centrally massed ellipsoidal bodies of yellowish brown color. At cyst formation the body rounds up within an irregularly lobed, thorny, cellulose cyst.

Dimensions.—Length, 22.2$\mu$ (20.6–25$\mu$); transdiameter, 16.9$\mu$ (12–21$\mu$).

Occurrence.—Figured by Ohno (1911) from fresh-water ponds in the Botanical Gardens of the University at Tokyo, Japan, where it was most abundant during the winter months.

Discussion.—The presence of three flagella in this form, two of which are longitudinal, if valid, is without parallel in the Dinoflagellata, and this fact raises the question of the correctness of Ohno's interpretation. The appearance shown in his figure 5, plate 1, is one commonly seen in living *Gymnodinium*. The actively moving flagellum swings through an arc that is fairly constant and forms a cone of rotation, the sides of which are strongly marked and give the appearance of two very distinct flagella. Watching these until the movement slows down, however, the observer sees them resolve into a single flagellum. The presence of three flagella in the stained specimen finds its parallel in conditions during the mitotic period in other flagellates. In most if not all flagellates the motor organelles are the first to exhibit signs of division, and this not infrequently results in a precocious outgrowth of the new flagella. In the material studied by Ohno rapid multiplication was evidently taking place, both in encysted and free swimming forms. The central part of the body is figured only as a dark mass and hence offers no conclusive evidence either way for the solution of this problem. It is evident, however, that Ohno's interpretation

can not be accepted even with reservations until the subject has received further investigation. It is highly probable that this species has the equipment of flagella normal to the Dinoflagellata.

*G. biciliatum* belongs to the subgenus *Gymnodinium*.

Comparisons.—In size, proportions, and color this species approaches *G. bogoriense* Klebs and *G. aeruginosum*, though not the figure selected by Schilling (1913) as typical. It is somewhat smaller than the average, 22.2μ, and smaller than *G. aeruginosum*, which Schilling (1913) states to have a length of 33–34μ, and is also relatively stouter. Cyst formation has some features in common in the two species, but the rigid irregularly spinose cyst of Ohno's species is apparently different from the imperfectly known cyst of *G. aeruginosum*. Its dimensions are very close (22.2μ by 16.9μ) to those of Klebs's (1912) species (22μ by 17μ), and the two may prove on full examination of chromatophores and cysts to be identical. If so Ohno's (1911) name has priority over that of Klebs (1912).

## **Gymnodinium bicorne** sp. nov.

Plate 2, figure 14; text figure BB, 10

Diagnosis.—This is a small species with subreniform body, its length 2.86 dorsoventral diameters; girdle submedian, displaced twice its own width; sulcus extending from near apex to antapex; color yellowish grey. Length, 63μ. Pacific off La Jolla, California, July.

Description.—The body is slender ellipsoidal, with broad apices, subreniform in lateral view, its dorsoventral diameter slightly greater than its transdiameter, its length 2.86 dorsoventral diameters at its widest part. The epicone and hypocone are subequal in length. The epicone is rounded conical in ventral view with broad apex; in lateral view the dorsal side is convex, the ventral concave posteriorly, convex anteriorly. It has a length on the left and right sides of 0.42 and 0.54 of the total length of the body respectively. The hypocone is somewhat narrower posteriorly than the corresponding part of the epicone. The antapex is rounded without sulcal notch.

The girdle is submedian in position, with a distance from the apex at its proximal and distal ends of 0.42 and 0.54 of the total length of the body respectively. The furrow has a width of about 0.09 transdiameter and is deeply impressed with smoothly rounded borders. Its course is that of a descending left spiral, with its distal end displaced posteriorly about twice its own width.

The sulcus is a narrow trough extending from near the apex to the antapex in an almost straight line. Its greatest width is found in the intercingular area, becoming narrower on the epicone and hypocone and fading out near both apices. The anterior flagellar pore opens at the proximal junction of the girdle and sulcus, the posterior pore a short distance below the distal one.

The nucleus is an ellipsoidal body lying in the central plane with its major axis parallel to the major axis of the body. It is filled with moniliform chromatin strands. Its major and minor axes are about 0.86 and 0.36 transdiameter in length respectively.

The plasma is finely granular and contains numerous small green granules and dark refractive bodies. An irregular, sacklike pusule opens into the anterior flagellar pore. The color of the cytoplasm is pearl grey with yellow splashes through it that may be chromatophores. This

organism was enclosed in a crescent-shaped double-contoured cyst much more arcuate than that of *G. lunula* and longer from tip to tip. Both flagella were active while under observation, producing a slight rotation of the body in the cyst.

DIMENSIONS.—Length, 63μ; dorsoventral diameter, 22μ; axes of nucleus, 19μ and 8μ; length of cyst, 105μ.

OCCURRENCE.—This was taken in a surface haul at the end of the pier at the Biological Station at La Jolla, California, July 19, 1917.

COMPARISONS.—This species greatly resembles an individual shown in Dogiel's (1906) figure 20, plate 1, which he includes in *Gymnodinium lunula*. The shape of the body is slightly different in the two forms included by Dogiel, the one referable to *G. bicorne* having a greater convexity of the dorsal and concavity of the ventral surfaces. The differences are probably adequate for specific distinction. Both Dogiel's figure 20 and our individual differ widely from *G. lunula*, in size and shape of the body as well as in their relative proportions. The shape of the enclosing cyst is apparently the only ground for its inclusion by Dogiel with those of *G. lunula*, and even this shows distinguishing characteristics.

## **Gymnodinium bifurcatum** sp. nov.

Text figures AA, 2, 3

DIAGNOSIS.—A large species with a peculiarly laterally flattened body, broadly ovoidal in side view, double funnel-shaped in ventral view, its length 1.07 dorsoventral diameters; hypocone dorsoventrally deeply bifurcate by the sulcus; girdle submedian, displaced one width; sulcus short and very deep on hypocone; color, pinkish grey. Length, 125μ. Pacific off La Jolla, California, August.

DESCRIPTION.—The body is broadly ovoidal in lateral view, widest anteriorly in the posterior epicone, strongly laterally compressed, especially on each side of the girdle region. Its length is 1.07 dorsoventral diameters at the widest part. Its transdiameter through the girdle region is about 0.56, through the midpart of the epicone about 0.12, and of the hypocone 0.15 of the dorsoventral diameter. The epicone and hypocone are subequal in length, but its broader dorsoventral diameter gives to the epicone a somewhat greater size. The epicone is subsemicircular in outline viewed laterally, with a very slight asymmetry on the ventral side. In ventral view it is inverted funnel-shaped, flaring widely in the posterior third of its length. Its length on the left and right sides is about 0.53 and 0.50 respectively of the total length of the body. The apex is smoothly rounded. The hypocone has the shape of a broad, rounded cone of about 70° in lateral view, with broad, rounded antapex. In ventral view it is bifurcate funnel-shaped, the cleft formed by the sulcus extending nearly its entire length to within a girdle's width of the girdle itself.

The girdle is submedian, the distance of its proximal and distal ends from the apex being 0.53 and 0.50 respectively of the total length of the body. It passes around the body with only a slight posterior deviation from a transverse direction in the distal fourth of its course, with a displacement of about its own width. The furrow is wide, about 0.04 transdiameter in width, and deeply impressed with smooth borders, of which the anterior one is prolonged into a thin,

finlike extension which covers about 0.7 of the width of the girdle. The transverse flagellum traverses nearly its entire length. The sulcus does not invade the epicone. On the hypocone it sinks through the body to the dorsal surface, dividing the hypocone into two subequal extensions or flaps (text figure AA, 3). The anterior flagellar pore opens at the proximal end of the girdle, the posterior pore slightly below the distal end.

The nucleus is an ellipsoidal body located in the central part of the organism, with its long axis lying in a dorsoventral plane. Its major and minor axes are about 0.39 and 0.24 dorsoventral diameter respectively.

The cytoplasm is unusually clear and transparent, the granulations being too fine to be easily detected. The ectoplasm is not marked off by a clear-cut line as in *G. dogieli,* yet it seems to have a slightly different consistency from that of the endoplasm and is more homogeneous. Below this layer in the epicone is a zone filled with small vacuoles. The remainder of the cytoplasm showed no cell inclusions. The surface of the hypocone is marked by a few lines, three on one face, which fade out near the girdle and the antapex. On the epicone these are more numerous and are shorter, being radially arranged around the margin in lateral view. The color of the organism is pinkish grey, deeper on the epicone and through the girdle region, though this latter may be due solely to the greater thickness of the body at that plane.

Dimensions.—Length, 125μ; transdiameter at girdle, 67μ; dorsoventral diameter, 109μ; axes of nucleus, 60μ and 30μ.

Occurrence.—This was found August 6, 1917, in a haul with a No. 25 silk net, 4 miles off La Jolla, California, in a haul from 60 meters to the surface and in a surface temperature of 21°2 C.

Comparisons.—This organism is a baffling one in attempting to trace out its affinities and even some details of its structure. Owing to its peculiar shape and delicacy of organization a camera drawing could not be obtained of the ventral view, the figure given in text figure AA, 3, being made free-hand and its measurements checked up with the camera sketch afterwards. In ventral view it greatly resembles a *Peridinium* escaped from its theca, but a lateral view serves only to emphasize the very great differences between it and any known *Peridinium.* In its lateral compression it recalls *Amphidinium sulcatum* sp. nov. (fig. U, 26), but differs greatly in all other details of its structure from that species. Its internal cytoplasmic organization is relatively simple, its thickened periplast, however, placing it in the subgenus *Pachydinium.* In its coloring it is not unlike *G. abbreviatum* sp. nov. (fig. Z, 7) in the same subgenus.

## **Gymnodinium bogoriense** Klebs

Text figure X, 10

*Gymnodinium bogoriense* Klebs (1912), pp. 397, 419, 439, fig. 7*c, d.*
*G. bogoriense,* Cavers (1913), p. 182, fig. $9_2$.
*G. bogoriense,* Pascher (1916), p. 127.

Diagnosis.—A minute species with ovoidal, dorsoventrally flattened body, its length 1.3 transdiameters; girdle without displacement; sulcus extending from girdle to antapex. Length, 23μ. Fresh-water ponds in the Botanical Garden at Buitenzorg, Java.

Description.—The body is stout ovoidal in ventral view, flattened dorsoventrally, its length 1.3 transdiameters at the widest part and its dorsoventral diameter 0.75 transdiameter. The epicone and hypocone are subequal in length, the greater width of the hypocone giving it a slightly greater volume. The epicone is subhemispherical in outline, its length about 0.43 of the total length of the body. The hypocone is more symmetrical than the epicone, broad and rounded posteriorly.

The girdle is slightly premedian in position and forms a complete circle around the body. The furrow is wide, about 0.2 transdiameter, and rather deeply impressed. The sulcus extends from the girdle to the antapex as a wide furrow which is slightly deflected to the left posteriorly. The flagellar pores are not indicated in Klebs's (1912) figures.

The nucleus is a small, spheroidal body near the central part of the cell. Its diameter is 0.3 transdiameter of the body. A number of radially arranged, stout rod-shaped bodies are found in the cytoplasm similar to the chromatophores in *G. rotundatum,* but their function is not mentioned in the description of Klebs (1912).

Dimensions.—Length, 20–24$\mu$; transdiameter, 16–18$\mu$; dorsoventral diameter, 12$\mu$; diameter of nucleus, 6$\mu$.

Occurrence.—This species was figured by Klebs (1912) from fresh-water ponds in the Botanical Garden at Buitenzorg, Java.

Comparisons.—This species greatly resembles *G. rotundatum* Klebs (1912), differing from it, however, in being flattened dorsoventrally and of somewhat smaller size, as well as being, in so far as known, a tropical species. Their description in the same paper by the veteran protistologist and investigator of the Dinoflagellata is an adequate guaranty of their specific distinctions. Its resemblance to Ohno's (1911) *G. biciliatum* has already been discussed.

## **Gymnodinium canus** sp. nov.

Plate 4, figure 41; text figures Z, 1, 2

Diagnosis.—A large species with asymmetrical ovoidal body, its length 1.72 transdiameters, epicone sloping anterodorsally, with an apical horn; girdle submedian, displaced 0.18 transdiameter; sulcus extends from apex to antapex; surface coarsely striate; color greenish grey. Length, 112$\mu$. Pacific off La Jolla, California, August.

Description.—Body large, asymmetrically ovoidal in lateral view, widest posteriorly, its length 1.72 transdiameters at the widest part, which is in the anterior third of the hypotheca. The ventral aspect presents an approximately symmetrical outline. In lateral view it is seen that the dorsoventral diameter, which equals the transdiameter posteriorly, in the epicone diminishes towards the apex which is eccentrically placed near the dorsal face of the body. The ventral surface forms an angle of about 50° with the transverse plane for about 0.7 of the height of the epicone, beyond which the slope approaches the transverse direction again for a short distance, then ascends longitudinally to the contracted, obliquely truncate and notched apex. The dorsal face of the epicone forms a slightly convex line from girdle to apex. Owing to the diminished dorsoventral diameter the epicone is considerably smaller in size than the hypocone, though their relative lengths are about the same. The length of the epicone on the left and right sides is about 0.43 and 0.53 respectively of the total length of the body. In ventral view it is dome-shaped with rounded sides; the apex is contracted and elongated with a slight twist

towards the right side of the body and deeply notched by the anterior end of the sulcus. The hypocone is slightly asymmetrical with the left side more convex than the right. It is bifurcated at the posterior end by the deep excavation of the sulcal notch which reaches through and cuts the dorsal surface of the body.

The girdle is submedian in position, its proximal end joining the sulcus at a distance from the apex of 0.43 and its distal end 0.53 of the total length of the body. It follows a descending left spiral course around the body, displacing its distal end posteriorly 0.18 transdiameter. The furrow is wide, about 0.09 transdiameter, and deeply impressed with smooth, overhanging borders. The sulcus extends from the apex to the antapex in a slightly sinuous line, and deeply notches both apices. The trough is narrow and shallow anteriorly, but expanding laterally and sinking deeper into the body posterior to the girdle until it nears the antapex where it reaches through and cuts the dorsal surface, bifurcating the posterior end of the body. The anterior flagellar pore opens at the proximal junction of the girdle and sulcus, the posterior pore somewhat behind the middle point between the distal junction and the antapex.

The nucleus is a large, ellipsoidal body in the center of the hypocone. In the specimen examined its nuclear structure could not be determined with any degree of accuracy. Its major and minor axes are about 0.49 and 0.3 transdiameter rsepectively. A small sacklike pusule opens into the posterior flagellar pore. None was noted at the anterior pore.

The cytoplasm is coarsely granular, somewhat dense, with closely packed vacuoles filling the entire central part of the body. A mass of minute, highly refractive granules lies in the region of the anterior flagellar pore. The cytoplasm and most of the vacuoles are grey in color, others showing a faint tinge of salmon pink. The surface is covered with longitudinal, equidistant, blue-green striae, approximately equal in number on both epicone and hypocone. Minute blue-green spherules are profusely scattered through the peripheral layer between the striae.

Dimensions.—Length, $112\mu$; transdiameter, $65\mu$; major and minor axes of nucleus, $32\mu$ and $20\mu$ respectively.

Occurrence.—A single individual was taken August 17, 1917, with a No. 25 net, 0.75 of a mile off La Jolla, California, in a haul from 80 meters to the surface and in a surface temperature of 22°5 C.

Comparisons.—This species, while not exhibiting the distinct ectoplasmic differentiations of *G. dogieli*, yet possesses a periplast of firmer consistency than any member outside of the subgenus *Pachydinium*, and it is therefore placed in that group. It stands near *G. costatum*, differing from it in its proportions and in the contracted shape of the epicone. In the marked asymmetry of its epicone it stands apart from all other species of *Gymnodinium*, though the lateral displacement of the apical point in such species as *G. hamulus* sp. nov., *G. agile* sp. nov., and *G. vestifici* Schütt (fig. Y, 5, 9, 10) is indicative of asymmetrical tendencies.

## **Gymnodinium carinatum** Schilling

Text figure X, 34

*Gyminodinium carinatum* Schilling (1891), p. 278, pl. 10, fig. 12.
*G. carinatum,* Mez (1898), p. 216.
*G. carinatum,* Lemmermann (1900), p. 116; (1903), p. 260.
*G. carinatum,* West (1916), fig. 36A.

Diagnosis.—A minute species with ellipsoidal body, its length 1.5 transdiameters; girdle without displacement; sulcus extending from girdle to antapex,

keel at its left; brownish chromatophores. Length, 39.7μ. In swamps near Neudorf, Switzerland.

DESCRIPTION.—The body is ellipsoidal, widest at the middle and tapering anteriorly, its length 1.15 transdiameters. The epicone and hypocone are subequal in length. The epicone is subconical with broad, blunt apex. Its length is about 0.5 the total length of the body. The hypocone is slightly narrower near the girdle and broader posteriorly than the corresponding parts of the epicone, with truncate or notched antapex.

The girdle forms a complete circle near the middle of the body, its distance from the apex being 0.5 of the total length of the body. It has a width of 0.1 transdiameter and is deeply impressed with rounded borders. The sulcus extends from the girdle to the antapex. Its left border is guarded by a well developed list or projecting keel. The transverse flagellum arises at the junction of the girdle and sulcus and the posterior flagellum slightly below.

The nucleus is not figured by Schilling (1891). The central part of the body is occupied by a few relatively large, disklike, light to dark brown chromatophores.

DIMENSIONS.—Length, 39.7μ; transdiameter, 34.5μ, as given in the text (Schilling, 1891), but the careful measurement of Schilling's drawings (1891, 1913) gives a width of 26μ. This size has been used in finding the proportions given in the description above.

OCCURRENCE.—Figured by Schilling (1891) from fresh-water swamps and ponds near Neudorf, Switzerland.

COMPARISONS.—This species presents a striking similarity to *G. aeruginosum*, *G. palustre*, and *G. viride* in size and proportions. It differs from them, however, in its shortened dorsoventral diameter and in the list on the left border of the sulcus. It belongs to the subgenus *Gymnodinium* and with the small group of fresh-water species in that subgenus, comprising *G. bogoriense*, *G. rotundatum*, *G. palustre*, *G. uberrimum*, *G. viride*, and *G. aeruginosum*.

## **Gymnodinium cinctum** sp. nov.

Plate 7, figure 75; text figure X, 28

DIAGNOSIS.—A minute species with ovoidal body, its length 1.18 transdiameters; girdle premedian, displaced nearly twice its own width; sulcus short; ellipsoidal yellow ochre chromatophores. Length, 25μ. Pacific off La Jolla, California, July.

DESCRIPTION.—This species has a minute, broadly ovoidal body, rounded at both apices, widest posteriorly, its length 1.18 transdiameters at the widest part. The hypocone greatly exceeds the epicone in size, having a greater width and exceeding it in length by 0.15 of its own length. The epicone is subconical (about 70°) with rounded, blunt or slightly pointed apex. Its greatest transdiameter is 0.63 transdiameter of the hypocone. It has a length on the left and right sides of 0.34 and 0.53 respectively of the total length of the body. The hypocone is midway between spherical and hemispherical in outline with broad, rounded antapex.

The girdle is premedian in position, its proximal end meeting the sulcus at a distance from the apex of 0.34 and its distal end 0.53 of the total length of the body. It sweeps around the body in a descending left spiral direction, displaced posteriorly at its distal end nearly twice its own width. The furrow is relatively wide, about 0.13 transdiameter, and deeply impressed with

smooth rounded borders. The sulcus is short on both epicone and hypocone, broad anteriorly and narrowing to a point posteriorly. In several individuals it extended posteriorly to the antapex. The anterior flagellar pore opens at the proximal junction of the girdle and sulcus, the posterior pore slightly below the distal junction.

The nucleus is ellipsoidal, its major axis coinciding with the major axis of the body, and is centrally located. Large monliform chromatin threads followed its major axis. Its major and minor axes are 0.77 and 0.54 transdiameter respectively.

A very large, irregular, sacklike pusule opens into both flagellar pores. The cytoplasm is clear and without visible granulations or color. A very few green oil droplets were present. Numerous ellipsoidal, disklike chromatophores are scattered through the peripheral layer. These have a general tone of yellow ochre. The organism is closely invested with a thin-walled, hyaline cyst which follows the contour of the body.

DIMENSIONS.—Length, 26$\mu$; transdiameter, 22$\mu$; axes of nucleus, 17$\mu$ and 12$\mu$.

OCCURRENCE.—It was first met with July 21, 1906, at La Jolla, California, in a haul made with a No. 20 net from 565 meters to the surface. One individual was taken July 5, 1917, with a No. 12 silk net, 6 miles off La Jolla, in a haul from 80 meters to the surface in a surface temperature of 21°4 C. It was found again July 23, at approximately the same place, with the same apparatus and in a surface temperature of 20°2 C.

COMPARISONS.—This species shows some slight resemblances to *Gymnodinium marinum* Kent. It differs from that species, however, in its proportions, its smaller epicone, reduced sulcus, and in its possession of yellow ochre chromatophores. No food masses were observed in the cytoplasm and the presence of chromatophores would suggest a holophytic mode of nutrition. Saville-Kent's (1880–82) species is holozoic. He observed it actively feeding on minute flagellates in the same culture. It belongs in the subgenus *Gymnodinium*.

## Gymnodinium coeruleum Dogiel

Text figure Z, 4

*Gymnodinium coeruleum* Dogiel (1906), pp. 35, 36, 40, pl. 2, figs. 46–47.
*G. coeruleum,* West (1916), p. 52.

DIAGNOSIS.—A rather large species with body subellipsoidal, its length about 2 transdiameters; epicone and hypocone subequal approaching spheroidal form; girdle submedian, displaced 0.28 transdiameter, sulcus extending from near the apex to the antapex; surface striate; color, cornflower blue. Length, 115$\mu$. Mediterranean Sea off Naples, June (?).

DESCRIPTION.—The body is stout subellipsoidal with broad apices, nearly circular in cross-section, its length about 2 transdiameters at the widest part. The epicone and hypocone are subequal and both are broadly rounded. The epicone is rounded with hemispherical apex. It has a length on the left and right sides of about 0.4 and 0.5 respectively of the total length of the body. The hypocone is somewhat less symmetrical than the epicone and a trifle more elongated and deeply notched at the antapex by the distal end of the sulcus.

The girdle joins the sulcus proximally at a distance from the apex of about 0.4 and distally 0.5 of the total length of the body. It follows a descending left spiral course about the body,

displaced posteriorly 0.28 transdiameter. The sulcus rises on the epicone near the apex and passes posteriorly in a sinuous line to the antapex. Near the posterior part it sinks deeply into the body in a wide depression and forms a deep notch on the ventral face of the antapex. The flagella and pores were not observed by Dogiel (1906).

The nucleus is an ellipsoidal body in the middle of the hypocone, filled with coarse, chromatin strands and three large masses of chromatin. Its major and minor axes are 0.48 and 0.37 transdiameter respectively. Brownish food masses were present in the anterior part. The surface is striate with longitudinal equidistant lines or ribs with slight depressions between them. On each side of the ribs, serially arranged, are small, oval platelike chromatophores, cornflower blue in color.

Dimensions.—Length, 107–115μ; transdiameter, 55–58μ; axes of nucleus, 28μ and 20μ.

Occurrence.—Figured by Dogiel (1906) from the Mediterranean off Naples. Two individuals were taken by him, one from a surface haul, the other from a depth of 50 meters. It was taken frequently in the plankton off La Jolla, California, in the summer of 1906 during an outbreak of red water caused by *Gonyaulax*.

Comparison.—This species has the same definite ectoplasm as that found in *G. gracile*, but not so highly differentiated as that in *G. pachydermatum*. It stands alone among the Dinoflagellata in its superb cornflower-blue coloring. A faint bluish tinge is sometimes seen in *G. gracile*, otherwise this color is entirely absent in all other species thus far described. Its thickened periplast places it in the subgenus *Pachydinium*, but its color isolates it. Structurally it is nearest *G. wilczeki* Pouchet (fig. Z, 8), a smaller stouter species with more deeply incised postmargin, and greater differentiation of epicone and hypocone.

## **Gymnodinium conicum** nom. sp. nov.

Text figure X, 27

*Gymnodinium viridis* Lebour (1917*b*), p. 189, fig. 4.

Diagnosis.—This is a small species with subovoidal body, its length 1.86 transdiameters; girdle premedian, displaced 0.2 transdiameter; sulcus extending from apex to antapex; greenish yellow chromatophores. Length, 60μ. Plymouth Sound, England, June.

Description.—The body is somewhat asymmetrical, ellipsoidal posteriorly, conical anteriorly, its length 1.86 transdiameters at the widest part. The transverse and dorsoventral diameters are nearly equal. The hypocone greatly exceeds the epicone in size, its length being greater by 0.36, with a continuously wider transdiameter. The epicone has the shape of a cone of about 80°, with a broad, blunt apex and slightly concave sides. It has a length on the left and right sides of about 0.16 and 0.19 respectively of the total length of the body. The sides of the hypocone are subparallel, in ventral view, rounding posteriorly. In lateral view the ventral side is nearly straight, the dorsal side convex. The antapex is broad and rounded with a deep trough on the ventral face.

The girdle is premedian in position. Its distance from the apex on the left and right sides is 0.16 and 0.19 respectively of the total length of the body. Its path is that of an irregularly

descending left spiral. The first part of its course makes a short, abrupt posterior turn, beyond which it turns anteriorly until it reaches the dorsal side. It passes across this in a nearly transverse direction, turning posteriorly on the ventral face, joining the sulcus with a posterior displacement of 0.2 transdiameter. The furrow is wide, about 0.06 transdiameter, and deeply impressed. The sulcus extends in a sinuous line from the left side of the apex to the antapex. On the hypocone it lies at the base of a deep trough which indents the ventral face. The sides become widely deflected near the antapex. The anterior flagellar pore evidently opens at the proximal junction of the girdle and sulcus, the posterior pore near the distal junction.

The nucleus is a large, ellipsoidal body in the anterocentral part of the hypocone. Its major and minor axes are 0.73 and 0.6 transdiameter respectively. The remainder of the cytoplasm is filled with numerous, greenish yellow chromatophores.

DIMENSIONS.—Length, 60µ; transdiameter, 32µ; axes of nucleus, 32µ and 19µ.

OCCURRENCE.—This species was figured by Lebour (1917*b*) from a single specimen taken in June from the waters of Plymouth Sound, England.

COMPARISONS.—This form is evidently one of the connecting links between *Amphidinium* and *Gymnodinium*, as shown in its structure. The epicone, however, has a relative length too great to include it with *Amphidinium*. This form and the one described by Lebour (1917*b*) as *Gymnodinium pseudonoctiluca* are separated mainly by size and a slight variation in color. It belongs in the subgenus *Gymnodinium*.

SYNONYMY.—The name, *G. viridis*, assigned to this species by Miss Lebour (1917*b*), is preoccupied by Penard's (1891) species, *G. viride*. We therefore propose for Lebour's species the name *G. conicum*.

## **Gymnodinium contractum** sp. nov.

Plate 5, figure 52; text figure X, 2

DIAGNOSIS.—A small species with subovoidal body, its length 1.43 transdiameters; girdle submedian, without displacement; sulcus on hypocone only; surface on epicone furrowed; plasma green with rose red granules. Length, 63µ. Pacific off La Jolla, California, August.

DESCRIPTION.—The body is subovoidal, with broad apices, nearly circular in cross-section, widest anteriorly, its length 1.43 transdiameters at the widest part. The epicone exceeds the hypocone in size, its length being greater by about 0.14 of itself, and its transdiameter somewhat greater. The epicone is subhemispherical in outline with the apex protruding slightly beyond the broad curve of the anterior part of the body. Its length is 0.52 of the total length of the body. The hypocone is somewhat narrower than the epicone, sharply contracted a short distance below the girdle to 0.77 transdiameter of the epicone. It expands slightly posteriorly, where it is rounded with deeply notched antapex.

The girdle is submedian in position, its distance from the apex about 0.52 of the total length of the body. The furrow is wide, about 0.08 transdiameter in width, and deeply impressed with smooth, overhanging borders. It forms a complete circle around the body without displacement. The sulcus extends from the girdle posteriorly to the antapex. It forms a shallow channel anteriorly and about midway of its length widens and at the same time sinks deeply into the body, deeply excavating the ventral surface of the antapex. The anterior flagellar pore opens at the junction of girdle and sulcus, the posterior pore about two widths of the girdle posterior to that point.

The nucleus is a large ellipsoidal body in the anterior part of the organism. It is filled with fine, moniliform chromatin strands. Its major and minor axes are about 0.47 and 0.36 transdiameter respectively. A sacklike, bilobed pusule opens into the anterior flagellar pore. The cytoplasm is finely granular, clear and transparent. Nutrition is holozoic, as the presence of two large food masses indicates. One of these is yellow ochre in color and the other bluish grey. Scattered through the body are minute, dark, highly refractive granules. The color of the plasma is a diffuse, light fluorite green with minute, rose red granules congregated at the apical or antapical regions or both.

The surface of the hypocone is smooth, that of the epicone is marked by longitudinal furrows outlined by green lines. These are sometimes deeply impressed, and are short, fading out at the girdle and near the apex.

Dimensions.—Length, 63–89$\mu$; transdiameter, 44–58$\mu$; axes of nucleus, 21$\mu$ and 16$\mu$.

Occurrence.—This was taken August 6, 1917, with a No. 25 silk net, 4 miles off La Jolla, California, in a haul from 60 meters to the surface and in a surface temperature of 21°2 C. On August 8 it was found at approximately the same place, in a haul from 80 meters to the surface and a surface temperature of 22°5 C. On August 15 five individuals were observed in a haul 0.75 of a mile off La Jolla from 80 meters to the surface.

Comparisons.—This species is closely related to *G. sulcatum* and *G. rubricauda* in its coloring and general appearance, yet differs in its relative proportions and its surface markings. It belongs in the subgenus *Gymnodinium*.

### **Gymnodinium corpusculum** (Perty) Saville-Kent

Text figure BB, 14

*Peridinium corpusculum* Perty (1852), p. 162, pl. 7, fig. 14.
*Gymnodinium corpusculum*, Saville-Kent (1880–82), p. 443.

Description.—A minute form with ovoidal or ellipsoidal body, the length 1.3 transdiameters. The girdle is near the posterior end, making the epicone much larger in size than the hypocone. The color is light brown or greenish yellow. Length, 13$\mu$. Fresh water in Switzerland.

Synonymy.—This was figured by Perty (1852) as *Peridinium corpusculum* and the name changed to *Gymnodinium corpusculum* by Saville-Kent (1880–82). Perty's figures lack sufficient morphological characters to establish it as a good species. Its affinities seem to be with *Gymnodinium*, near *G. musei*, but available data render it unidentifiable and it must be placed in species *incertae sedis* until further investigation shall rediscover it and make its status definite.

### **Gymnodinium costatum** sp. nov.

Plate 3, figure 33; text figure Z, 10

Diagnosis.—A large species with subovoidal body, its length 1.66 transdiameters: girdle submedian, displaced 0.22 transdiameter; sulcus extending from apex to antapex; surface ridged; color, greyish pink. Length, 150$\mu$. Pacific off La Jolla, California, June to August.

DESCRIPTION.—The body is large, subovoidal, widest near the equator with rounded apices, circular in cross-section, its greatest length 1.66 transdiameters at the widest part. The epicone exceeds the hypocone in size, its length being greater by 0.2 of its own length. It is dome-shaped with symmetrically rounded sides and broad, slightly crenulated apex. It has a length on the left and right sides of 0.5 and 0.62 respectively of the total length of the body. The hypocone is narrower than the epicone with its sides less rounded, tapering posteriorly to the broad, truncate antapex. This is deeply excavated by the sulcal notch and its borders crenulated by the surface ridges terminating in the furrow.

The girdle forms a descending left spiral with a posterior displacement of its distal end of 0.22 transdiameter and an overhang of about 0.07 transdiameter. Its proximal end joins the sulcus at a distance from the apex of 0.50 and its distal end 0.62 of the total length of the body. The furrow is wide, about 0.07 transdiameter and deeply impressed, the borders, especially on the anterior side, overhanging it, thereby reducing its apparent width by one-half. In some forms the crenate surface is in evidence along the borders of the girdle, in others the crenulations along the borders are obscure. The sulcus begins as a slightly enlarged pit at, or somewhat to the left of the apex, passes posteriorly to the girdle in an almost straight line and continues its course to the antapex in a sigmoid curve. The furrow is narrow anteriorly, enlarging to twice its width at the girdle and again behind the region of the posterior pore. Near the antapex it deepens to about 0.7 of the transdiameter of the body at that plane, forming a deep excavation at the antapex. The anterior flagellar pore opens at the proximal junction of the sulcus and girdle, the posterior pore a short distance below the distal junction.

The cell contents consist of a spheroidal nucleus, a cluster of subspheriodal bodies varying in color from light saffron yellow to dark orange yellow, small green rodlets and minute refractive granules. The nucleus is located in the anterior part of the hypocone, just behind the girdle and is filled with coarse, moniliform chromatin strands and a single minute, excentrically located nucleolus. Its axis is about 0.4 transdiameter in length. Large, spheroidal food masses were present in all individuals examined, with only slight variations in size, color, and position. Clustered around and among them were numerous dark purplish, highly refractive bodies. These are double-contoured and presumably fatty in nature. A greyish pink pervades the cytoplasm as a whole, fading out as the animal becomes moribund. A small club-shaped pusule is connected with the anterior flagellar pore by a long, slender canal.

The surface is regularly marked by stout, longitudinal, equidistant, yellowish striae. These are about the same in number on both epicone and hypocone, about 23 across the ventral face at the girdle, decreasing by extinction at various levels towards the apices, so that there is no considerable approximation of the striae in these regions. They lie in the troughs of shallow furrows, with rounded ridges between, which give a crenate appearance to the borders at the girdle and at the apices. The small, slender, green rodlets are arranged at irregular intervals along the ridges, at right angles to and immediately beneath the surface.

DIMENSIONS.—Length, 150–154$\mu$; transdiameter, 90$\mu$; diameter of nucleus, 20$\mu$.

OCCURRENCE.—This species was first seen July 16, 1906, in a surface haul with No. 20 net, 1 mile off La Jolla, California. One individual was taken June 25, 1917, with a No. 12 net in a haul 6 miles off La Jolla, from 80 meters to the surface and in a surface temperature of 18°3 C. It was found again on June 28 under approximately the same conditions. It was noted July 23 and thereafter was quite abundant, being found in most of the hauls taken up to August 13.

Comparisons.—This is one of the largest and at the same time most striking members of the genus *Gymnodinium*. While it lacks the highly differentiated, mammillated ectoplasm of *G. pachydermatum*, it possesses a thick periplast of much firmer consistency than the members of the other subgenera of the genus; it is therefore placed in the subgenus *Pachydinium*, near *G. canus* sp. nov., *G. coerulum*, Dogiel, *G. puniceum* sp. nov., and *G. wilczeki* Pouchet, all with somewhat ribbed, coarsely striate surface (figs. X, 1, 4, 5, 8). It is the largest of the group, lacks the contracted apex of *G. canus*, differs in color from *G. coeruleum*, has a proportionally larger epicone than *G. puniceum*, and wholly different proportions from *G. wilczeki*.

## **Gymnodinium cucumis** Schütt

Text figure Y, 16

*Gymnodinium cucumis* Schütt (1895), pp. 100, 108, 111, 116, 117, pl. 21, fig. 64.

Diagnosis.—A large species with slender fusiform body, its length 3.24 transdiameters; girdle with a descending left spiral course displaced about 2.5 of its own width; sulcus extending from apex to antapex; surface striate. Length, 210$\mu$. Mediterranean at Naples or the Atlantic.

Description.—The body is long, slender fusiform, slightly wider posteriorly, tapering at both ends, its length 3.24 transdiameters at the widest part. The epicone exceeds the hypocone by about 0.39 of its own length. It is conical (32°) in shape, slightly asymmetrical with a narrow, blunt apex. It has a length at its left and right sides of 0.55 and 0.6 respectively of the total length of the body. The hypocone is broader (45°) with a narrow, blunt antapex. Its length from the proximal and distal ends of the girdle is 0.4 and 0.32 respectively. The dorsoventral and transverse diameters are equal.

The girdle is postequatorial, meeting the sulcus proximally about 0.55 and distally 0.60 of the total length of the body from the sulcus. It follows a descending left spiral course, displaced posteriorly about 2.5 times its own width. It is a deeply imbedded furrow, 0.09 transdiameter in width with overhanging, ribbed borders. The sulcus extends from the apex to the antapex in an irregular line but with little or no torsion. The positions of the flagellar pores are not shown in Schütt's (1895) figures, though the longitudinal flagellum is shown, projecting from the distal end of the sulcus.

The nucleus is a relatively small, spheroidal body in the central part of the hypocone. Its axis is 0.4 transdiameter in length. A large sacklike pusule extends along the transverse plane of the body below the girdle, opening probably into one of the flagellar pores. A number of food bodies were shown in one of Schütt's figures (1895, pl. 21, fig. 64). The surface is striate with a strong tendency towards the formation of ridges between the striae.

Dimensions.—Length, 211$\mu$; transdiameter, 65$\mu$; diameter of nucleus, 26$\mu$.

Occurrence.—Figured by Schütt (1895) from the collections of the Plankton Expedition, presumably from the Mediterranean at Naples or the Atlantic. Its occurrence has not been recorded elsewhere.

Comparisons.—This is the second largest species in the genus or even in the Gymnodinioidae thus far described, one species only exceeding it in length, *G. dogieli*, with a length of 212$\mu$. In the presence of ribs between the striae on

the surface it resembles *G. costatum.* It belongs in the subgenus *Lineadinium,* in which no other species approximates it in size, proportions, or nature of the surface, except *G. costatum,* as above noted.

### **Gymnodinium diploconus** Schütt

Text figure Y, 6

*Gymnodinium diploconus* Schütt (1895), pl. 24, fig. 78.
*G. diploconus,* Schütt (1896), p. 5, fig. 5, B, C.
*G. diploconus,* Lemmermann (1899), p. 358; (1910), p. 618.
*G. diploconus* Entz, Jr. (1902), p. 92; (1905), p. 108.

Diagnosis.—A medium sized species, with biconical body with subtruncate apices, its length 1.24 transdiameters; girdle without displacement; sulcus extending from the girdle to the antapex; surface finely striate. Length, 57μ. Atlantic or Bay of Naples; Pacific off La Jolla, California, June, July.

Description.—The body is biconical, broadly flaring in the middle region around the girdle and tapering to the broadly subtruncate apices, its length 1.24 transdiameters at its widest part. It is nearly circular in cross-section. The hypocone and the epicone are subequal. The epicone is conical, about 55° in the anterior part, the posterior portion flaring at the girdle. It has a length of about 0.39 to 0.50 of the total length of the body. The conical portion of the hypocone is slightly narrower than the epicone (40°) with the anterior portion flaring broadly to meet the girdle. The antapex is blunt with a small sulcal notch. Our specimen (fig. Y, 6) is broader and stouter than that of Schütt (1895).

The girdle is premedian in position, having a distance of about 0.39 of the total length of the body from the apex or may be median and equatorial. It follows a circular path around the body with no posterior displacement or with a displacement of less than half its own width. The furrow is narrow and deeply imbedded with overhanging borders. The sulcus extends from the girdle to the antapex, following a slightly sinuous course. The anterior flagellar pore is located at the anterior junction of the girdle and sulcus, the posterior pore is about midway between the girdle and antapex.

The nucleus is a spherical body centrally located. Its diameter is about 0.24 transdiameter of the body in length. Numerous spherules of varying size are found in the hypocone, especially numerous at the antapex, and fewer in the epicone. Stout, rod-shaped, yellowish chromatophores are scattered through the peripheral zone. The surface is covered with fine longitudinal striae, about equal in number on both ends of the body, and about 30 across the ventral face.

Dimensions.—Length, 57–80μ; transdiameter, 46–63μ; diameter of nucleus, 12–20μ.

Occurrence.—This was figured by Schütt (1895) from the collections of the Plankton Expedition from the Bay of Naples or from the Atlantic. It also occurred at La Jolla, California, in collections made June 30, 1904, in a haul 12 miles offshore, from 300 meters to the surface, and on July 5, 1904, 10 miles offshore, in a haul from 290 meters to the surface.

Comparisons.—This belongs in the subgenus *Lineadinium,* and stands near *G. heterostriatum* nom. sp. nov. (fig. Y, 7), but has equal numbers of striae on both ends of the body. In the number and fineness of its striae it resembles *G. radiatum* sp. nov. (fig. Z, 9) and *G. multilineatum* sp. nov. (fig. Y, 18).

There is some question as to the identity of Schütt's species and our specimens. Our individuals (fig. Y, 6) were more rotund than his, and the sulcus extends to the apex, while in his figures it is limited to the hypocone. The surface striation is strikingly similar and for this reason we do not separate them.

### Gymnodinium dissimile sp. nov.

Plate 4, figure 35; text figure X, 32

DIAGNOSIS.—A small species with rotund ellipsoidal body, its length 1.17 transdiameters; girdle postmedian, displaced half its own width; sulcus extending from apex to antapex; color grey green. Length, 48$\mu$. Pacific off La Jolla, California, August.

DESCRIPTION.—The body is rotund, deeply constricted by the girdle, with broad apices, widest anteriorly, its length 1.17 transdiameters at the widest part. A cross-section of the body is nearly circular. The epicone greatly exceeds the hypocone in size, its length being greater by 0.46, its transdiameter by 0.07. The epicone is subspherical, occupying a sector about 210° of a sphere, with broad apex. It has a length on the left and right sides of 0.62 and 0.64 respectively of the total length of the body. The hypocone is constricted anteriorly by the girdle, rounded posteriorly with the antapex deeply notched by the distal end of the sulcus.

The girdle is situated posterior to the midplane of the body, with a distance from the apex on the left and right sides of 0.62 and 0.64 respectively of the total length of the body. It deeply constricts the body, the transdiameter of the girdle being about 0.8 of the greatest transdiameter of the body which is in the lower third of the epicone. It extends around the body in a nearly transverse direction with a slight posterior displacement on the right of about half its own width. The furrow is wide, about 0.07 transdiameter, and deeply impressed with smoothly rounded sides.

The sulcus begins a short distance below the girdle and extends posteriorly to the antapex. It is a shallow trough on the epicone, becoming deeper on the hypocone until near the antapex it reaches the dorsal border of the body, deeply notching that part of the hypocone. The anterior flagellar pore is found at the proximal junction of the girdle and sulcus and the posterior pore midway between that point and the antapex.

The nucleus is a relatively large, ellipsoidal body in the center of the organism. It is filled with coarse, moniliform, chromatin strands following its long axis. Its major and minor axes are 0.52 and 0.45 transdiameter in length respectively.

A small sacklike pusule opens into each flagellar pore. The cytoplasm is granular and grey green in color. A few vacuoles filled with a fluid colored like that in the pusules are found in the anterior part of the body. In the peripheral zone are numerous blue-green oil drops and dark, refractive granules. No striae or other surface markings were observed.

DIMENSIONS.—Length, 48$\mu$; transdiameter, 40$\mu$; axes of nucleus, 21$\mu$ and 18$\mu$.

OCCURRENCE.—A single specimen was taken August 3, 1917, 6.5 miles off La Jolla, California, with a No. 000 net, in a haul from 80 meters to the surface and in a surface temperature of 21°2 C.

COMPARISONS.—In size, proportion, larger epicone, constricted girdle, and posterior sulcal notch this species is very close to *G. contractum* sp. nov. (fig. X, 2), but differs from it in having the sulcus extended upon the epicone, in the absence of all striations, and in the absence of the reddish color.

## **Gymnodinium dogieli** sp. nov.

Plate 3, figure 34; text figures AA, 1, 8

DIAGNOSIS.—A large species with biconical body, its length 2.03 transdiameters: epicone concave; submedian girdle, displaced nearly its own width; sulcus extending from a short distance above the girdle to the antapex; differentiated ectoplasm; color orange yellow. Length, 193μ. Pacific off La Jolla, California, July, August.

DESCRIPTION.—The body is nearly biconical, slender campanulate anteriorly, wide posteriorly, with narrowly rounded apices, its length 2.03 transdiameters at the widest part. The epicone exceeds the hypocone in length by about 0.3 of its length, but being much narrower is less in volume. It forms a long, slender cone, the sides of which form an angle of about 18° with the longitudinal axis of the body anteriorly and in the posterior third an angle of about 43°. The sides are thus concave and symmetrical with narrowly rounded apex. Its length is about 0.56 of the total length of the body. The hypocone forms a broader cone, its sides forming an angle of about 35° with the longitudinal axis. At the girdle they flare out into a wide, shelflike extension to serve as its anterior border. The sides are symmetrically rounded with a broadly rounded antapex without sulcal notch.

The girdle is protuberant, located slightly posterior to the middle of the body, its distance from the apex being about 0.56 of the total length of the body on the right, slightly less on the left side. Its distal end is displaced posteriorly somewhat less than its own width. The furrow is wide, about 0.06 transdiameter, and is deeply impressed with widely overhanging borders, the proximal border cut under by the furrow, the distal gradually rounded. The sulcus invades the epicone for a very short distance only as a rather shallow furrow. Beyond the girdle it extends as a shallow trough in an almost straight line to the antapex, expanding slightly posteriorly, until at the antapical region its borders spread out to meet the posterior borders of the body on each side of the antapex. The anterior flagellar pore opens at the proximal junction of the girdle and sulcus, the posterior flagellar pore at about 0.3 of the distance from girdle to antapex.

The nucleus is a large ellipsoidal body in the posterior part of the hypocone. Its major and minor axes are about 0.4 and 0.27 transdiameter in length respectively.

A small, spherical pusule opens into the posterior flagellar pore through a long, slender canal. The cytoplasm is finely granular and is usually filled with various cell inclusions. In the central region near the anterior pore was a large group of small, highly refractive, double-contoured, dark greenish granules. Mingled with these were a number of yellowish spheroidal bodies, probably food masses. Above these and almost filling the epicone were large vacuoles of a faint bluish color, presumably of a fatty nature. At the apex were a smaller group of the same refractive spherules found in the central part of the body, with a group of radial, greenish rodlets. A second group of rodlets was found just above the girdle region and a third group of longer rodlets radiating out from the spherical part of the pusule. Partly filling the hypocone and reaching upward into the epicone were large vacuoles filled with a pink fluid like that found in the pusule.

The protoplasm is divided into distinct ectoplasm and endoplasm. The ectoplasm is about 4μ in thickness in the hypocone and slightly less in the epicone. It is composed of a thin, double-contoured layer, bright yellow in color, surmounted peripherally by an alveolar layer. The alveoli are rounded outwardly, giving to the outline of the body an uneven, wavy line. This layer is deep orange at the antapical region, shading to a lighter tone anteriorly. The color of the endoplasm is a greenish yellow with bluish tinges. The combination of colors in this species gives a rich Oriental effect, impossible adequately to describe or to reproduce with water colors.

Dimensions.—Length, 193μ to 212μ; transdiameter, 95μ to 110μ; major and minor axes of nucleus, 42μ and 26μ.

Occurrence.—The individual figured was taken June 27, 1917, with a No. 12 silk net, in a haul 6.1 miles off La Jolla, California, from 120 meters to the surface and in a surface temperature of 20°6 C. It was taken on July 20, 6 miles off La Jolla, and on July 27, 4 miles off La Jolla, with a No. 25 silk net, from 80 meters to the surface and in a surface temperature of 21° C. On August 13 it was quite abundant in a haul 0.75 miles off La Jolla from a depth of 83 meters and in a surface temperature of 21°9 C, 6 individuals being observed in a short examination of this catch.

Comparisons.—This is one of the largest species of *Gymnodinium* thus far described, the length of the longest individual observed, 212μ, being the greatest length on record, the nearest approach to it being *G. cucumis* with a length of 210μ. It is also one of the most highly differentiated species in the genus in its cytoplasmic structure, resembling in this respect *G. pachydermatum* sp. nov., *G. amphora* sp. nov., and *G. abbreviatum* sp. nov. (figs. AA, 5, 6; fig. Z, 7). Like them it is holozoic in nutrition, the presence of numerous green rodlets and masses of refractive bodies indicating a high degree of metabolism. It is one of the most striking, richly colored dinoflagellates found in the La Jolla region, sharing that distinction with *G. pachydermatum*, which it greatly resembles in color. It belongs to the subgenus *Pachydinium*, with these species, and differs from them in its longer, more attenuate epicone and less displacement of the girdle.

## **Gymnodinium doma** sp. nov.

Plate 5, figure 57; text figure X, 31

Diagnosis.—This is a small species with ovoidal body, its length 1.43 transdiameters; girdle premedian, displaced about twice its own width; sulcus short on both epicone and hypocone; color blue grey. Length, 59μ. Pacific off La Jolla, California, July.

Description.—The body is ovoidal with broad apices, circular in cross-section, widest anteriorly, its length 1.43 transdiameters at the widest part, which is at the girdle. The hypocone exceeds the epicone in size, its length being greater by about 0.23 of its own length, though its transdiameter is somewhat less. The epicone is hemispherical in outline with symmetrically rounded apex. It has a length on the left and right sides of 0.33 and 0.45 respectively of the total length of the body. The hypocone is elongate hemispherical, or campanulate in outline, flaring at the girdle, tapering slightly posteriorly with broad rounded antapex.

The girdle is premedian in position, its anterior junction with the sulcus occurring at a distance from the apex of 0.33 of the total length of the body. It passes around the body in a transverse direction for 0.75 of its course, beyond which it turns posteriorly and joins the sulcus at an angle of 70° with the main axis of the body. It is displaced about twice its own width. The furrow is wide, about 0.09 transdiameter in width, and is deeply impressed with smooth borders. The sulcus is short, beginning midway of the distance between girdle and apex on the epicone and extending posteriorly for about the same distance on the hypocone. Its course

is that of a sigmoid curve, forming a shallow trough which soon fades out. The anterior flagellar pore is found at the proximal junction of the girdle and sulcus, the posterior pore a very short distance beyond the distal junction.

The nucleus is elongated, somewhat reniform, its long axis coinciding with the short axis of the body. It is filled with rather large, moniliform chromatin threads following its long axis. Its major and minor axes are 0.6 and 0.36 transdiameter in length respectively.

A large, ellipsoidal pusule is situated in the posterior part of the hypocone and opens into the anterior flagellar pore by a long narrow tube. The cytoplasm is finely granular. Scattered through it are small vacuoles filled with fluid of the color of the pusule. Near the surface and at right angles to it are numerous small, greenish rodlets. A large yellowish food mass was found in the antapical region. The general color of the body is bluish grey, shading to orange in the peripheral zone. Nutrition is holozoic, as indicated by the presence of ingested food masses.

DIMENSIONS.—Length, 59μ; transdiameter, 41μ; axes of nucleus, 25μ and 15μ.

OCCURRENCE.—One individual was taken on July 2, 1917, with a No. 12 silk net in a haul taken 6 miles off La Jolla, California, from 20 meters to the surface and in a surface temperature of 21°4 C.

COMPARISONS.—In its peripheral zone of short radial rodlets this species resembles some species of *Gyrodinium*, such as *G. fissum* and *G. heterostriatum*, though the rodlets are fewer in number than in the case of the latter species. They are probably concerned with the metabolism of the cell. In the anterior location of the girdle and the consequent reduction in size of the epicone it resembles *G. fulgens, G. conicum,* and *G. pseudonoctiluca* (fig. X, 30, 27, 35). It belongs to the subgenus *Gymnodinium*, though its proportions are near to those of the striate species included in *Lineadinium* (fig. Y), especially to *G. gracile* Bergh (fig. Z, 3) and *G. heterostriatum* (fig. Y, 7). However, it is wholly devoid of striae. It resembles *G. rubescens* in size, displaced girdle, and short sulcus, but has a more tapering hypocone, and lacks chromatophores.

## **Gymnodinium filum** Lebour

Text figure X, 20

*Gymnodinium filum* Lebour (1917*b*), p. 193, fig. 9.

DIAGNOSIS.—A small, slender species with biconical body, its length 4.06 transdiameters; girdle anterior, without displacement; sulcus short on epicone, long on hypocone, reaching to within a short distance of the antapex; colorless. Length, 65μ. Plymouth Sound, England, July.

DESCRIPTION.—The body is long and slender, tapering to a threadlike point posteriorly, widest anteriorly, its length 4.06 transdiameters at the widest part. The dorsoventral diameter is slightly less than the transdiameter. The hypocone exceeds the epicone in length by about 0.74. The epicone is conical, about 60°, with narrow, blunt apex. Its length is about 0.2 of the total length of the body. The transdiameter of the base is very slightly greater than its height. The hypocone is long, slender conical, its angle about 20° and its length slightly more than three times its greatest transdiameter. The antapex is drawn out into a long, slender point.

The girdle is placed far anteriorly, its distance from the apex about 0.2 of the total length of the body. It forms a complete circle around the body without displacement. The furrow is about 0.12 transdiameter in width and deeply impressed. The sulcus begins about midway between the girdle and apex and extends posteriorly in a straight line to within a short distance of the antapex. The flagella and flagellar pores were not figured by Lebour (1917*b*).

The nucleus is ellipsoidal and is found in the posterior half of the hypocone. It is filled with loose chromatin strands. Its major and minor axes are about 0.68 and 0.37 transdiameters in length respectively. Nutrition is holozoic, as indicated by the large, irregular food mass near the center of the body. In Lebour's figures the surface is marked by lines, but these are evidently used as contour lines, since she states that the surface is without striae. The body is clear and colorless.

DIMENSIONS.—Length, 65μ; transdiameter, 16μ; axes of nucleus, 11μ and 6μ.

OCCURRENCE.—Figured by Lebour (1917*b*) from water samples collected in July at Plymouth Sound, England.

COMPARISONS.—This species shows the extreme of specialization in the genus in the attenuate form of the body. It is placed in the subgenus *Gymnodinium* because it lacks striae, the scattered longitudinal lines being interpreted as contour lines. Should striae be present, as they may be, the species should be transferred to the subgenus *Lineadinium*, where it would be grouped with other fusiform species, such as *G. cucumis* (fig. Y, 16). It is unique, whatever its allocation, with no closely resembling species in *Gymnodinium*.

## **Gymnodinium flavum** sp. nov.

Plate 9, figure 100; text figure X, 7

DIAGNOSIS.—This is a minute species with broadly ellipsoidal body, slightly compressed dorsoventrally, its length 1.21 transdiameters; girdle submedian, displaced about twice its own width; sulcus extending from girdle to antapex; strontium yellow chromatophores. Length, 31μ. Pacific off La Jolla, California, July, August.

DESCRIPTION.—The body is broadly ellipsoidal, almost globular in shape, with broad apices, its length 1.21 transdiameters at the widest part. It is slightly compressed dorsoventrally, its dorsoventral diameter being 0.93 transdiameter. The hypocone slightly exceeds the epicone in length. The epicone is hemispherical with smoothly rounded sides and broad apex. It has a length on the left and right sides of 0.28 and 0.41 respectively of the total length of the body. The hypocone also has a hemispherical outline with broad antapex slightly or not at all interrupted by the sulcal notch.

The girdle is slightly premedian in position. Its proximal end meets the sulcus at a distance from the apex of about 0.28, and its distal end 0.41 of the total length of the body. Its path around the body is that of a descending left spiral, with its distal end displaced posteriorly about twice its own width. The furrow is wide, about 0.06 transdiameter, but somewhat unequal throughout, and is deeply impressed. The furrow undercuts the anterior lip, gradually curving out posteriorly to meet the surface of the body. The sulcus rarely or never extends upon the epicone. It extends posteriorly to or near the antapex as a slightly sinuous line. Its width appears to be irregular. The left border projects more or less above the general surface and frequently forms an overlap partly covering the trough. This slightly raised appearance of

the left side can be traced into the epicone where the sulcus is absent as a distinct furrow. The anterior flagellar pore is found near the lower border of the proximal end of the girdle and sulcus. The transverse flagellum usually traverses the entire length of the girdle. The posterior pore is slightly posterior to the distal junction of the girdle and sulcus.

The nucleus is spheroidal, and situated below the girdle on the left side of the hypocone. Its axis is about 0.3 transdiameter.

The cytoplasm is clear and pearl grey in color. In the peripheral zones are leaflike chromatophores of strontium yellow color. These are quite variable in size and also in number, ranging from 2 to 20 or more. In the deeper parts of the protoplasm are numerous blue-green bodies, usually one large one in the posterior half of the body and much smaller ones located elsewhere. In the peripheral zone outside the layer of chromatophores are numerous, minute yellowish green rodlets, invisible under the low powers of the microscope. These may vary from a densely packed layer to a few scattered ones and are probably metabolic in origin. No striae or other surface markings were detected.

DIMENSIONS.—Length, 26–35$\mu$; transdiameter, 21–28$\mu$; diameter of nucleus, 10$\mu$.

OCCURRENCE.—This species was present in very great abundance during an outbreak of yellow water, July 27 to August 13, 1914, along the shore at La Jolla, California. No other organisms were present in any considerable numbers. In some surface hauls it was present almost to the exclusion of all other organisms, and in all the hauls made near the Biological Station at that season it was by far the most abundant form. It entirely disappeared from the hauls shortly after the cessation of the yellow water. A single individual was taken July 8, 1917, 4 miles off La Jolla, in a haul from 80 meters to the surface and in a surface temperature of 19°8 C.

PHOSPHORESCENCE.—During the occurrence of the yellow water above recorded there was a great display of phosphorescence in the breakers along the shore. A few *Gonyaulax* and *Noctiluca* were present in the hauls made, but in numbers far too small to account for this display. Unfortunately no laboratory tests were made to determine the luminescence of *Gymnodinium flavum*. It was, however, the only organism present in sufficient numbers to justify the claim made for it, i.e., that it is strongly luminscent.

COMPARISONS.—This species most nearly resembles the related arenaciphilous form, *G. agile,* from beach sands at La Jolla, but differs from it in the relative proportions of epicone and hypocone, in a smaller compression of the body and in the color of its chromatophores. It belongs to the subgenus *Gymnodinium.*

## **Gymnodinium fulgens** nom. sp. nov.

Text figure X, 30

*Gymnodinium pseudonoctiluca* Lebour (1917*b*), p. 188, fig. 3.

DIAGNOSIS.—A large species with stout, fusiform body, its length 2.27 transdiameters; girdle without displacement; sulcus extending from girdle to antapex; yellow chromatophores. Length, 100$\mu$. Plymouth Sound, England, June, July.

Description.—The body is stout fusiform, conical anteriorly and rounded posteriorly, its length 2.27 transdiameters at the widest part. The girdle is placed far anteriorly, dividing the body into two very unequal portions. The hypocone exceeds the epicone in length by 0.57 of its own length. The epicone is conical (80°) with a blunt apex which is deflected slightly to the dorsal side. The hypocone is rounded at the antapex in ventral view, in lateral view is asymmetrical, with dorsal side rounded and ventral flattened. On each side of the sulcus the body is drawn out into a flap with the left one slightly wider than the right.

The girdle forms a complete circle about the body at a distance from the apex of 0.29 of the total length of the body. The furrow is narrow with a shallow trough. The sulcus begins at the girdle and extends to the antapex. In the middle part of its course it is obscured by the overlapping of the drawn-out borders, which become widely deflected posteriorly.

The nucleus is an irregularly ellipsoidal body near the center of the hypocone. Its major and minor axes are about 0.57 and 0.40 transdiameters in length respectively. The body also contained two large food masses (?) and numerous bright yellow, elliptical chromatophores, those in the anterior half of the body being arranged in lines.

Dimensions.—Length, 100$\mu$; transdiameter, 44$\mu$; axes of nucleus, 25$\mu$ and 19$\mu$.

Occurrence.—Figured by Lebour (1917*b*) from collections made in June and July at Plymouth Sound, England.

Synonymy.—Described by Lebour (1917*b*) as *G. pseudonoctiluca* Pouchet, it presents some differences which separate it from that species, the most striking ones being in the form of the girdle and the presence of chromatophores. In Pouchet's (1885*a*) species the girdle turns posteriorly on the ventral surface, the opposite ends meeting slightly posterior to the middle of the body. In Lebour's form it passes around the body as a complete circle with little posterior deflection.

Comparisons.—Chromatophores are more frequently found in the freshwater species of *Gymnodinium* than in the marine forms. In this characteristic, together with the relative size of epicone and the anterior position of the girdle, it forms an intermediate species linking *Gymnodinium* to *Amphidinium*, but is not otherwise more primitive than species previously treated here. It belongs in the subgenus *Gymnodinium*.

## **Gymnodinium fuscum** (Ehrenberg) Stein

Text figure X, 19

*Peridinium fuscum* Ehrenberg (1834), pp. 270–271; (1835), pp. 126–127; (1838), p. 254, pl. 22, fig. 15, date quoted on p. 254 as 1833 (1832) by Ehrenberg.
*P. fuscum,* Dujardin (1841), p. 376.
*P. fuscum,* Riess (1842), p. 35.
*P. fuscum,* Perty (1852), p. 162.
*Heteraulacus fuscus,* Diesing (1850), p. 100; (1866), as *Heteroaulax fusca,* p. 95.
*Peridinium fuscum,* Bailey (1850), p. 46.
*P. fuscum,* Claparède and Lachmann (1858–61), p. 406.
*P. fuscum,* Maggi (1874), p. 118; (1880), p. 9.
*P. fuscum,* Stein (1878), pp. 2, 70, 72, 78, 88, 90. As *Gymnodinium fuscum,* (1878), pp. 95, 97; (1883), pl. 2, figs. 14–18.
*P. fuscus,* Eyferth (1879), p. 19.

*Gymnodinium fuscum*, Saville-Kent (1880–82), pp. 443, 463, pl. 25, figs. 17, 18.
*G. fuscum*, Bergh (1881*b*), p. 191.
*G. fuscum*, Klebs (1883), pp. 348, 351, 352, pl. 2, fig. 25 (in part, his figure is evidently a *Hemidinium*); (1884), p. 739; (1912), pp. 391, 421.
*G. fuscum*, Pouchet (1883), pp. 402, 445.
*Peridinium fuscum*, Griffith (1883), p. 587.
*Gymnodinium fuscum*, Bütschli (1885), pp. 925, 964, 986.
*G. fuscum*, Gadeau (1890), p. 30.
*G. fuscum*, Schilling (1891), pp. 248, 275, pl. 10, fig. 9; (1913), p. 15, fig. 10. After Stein (1883).
*G. fuscum* Levander (1894), p. 43; (1900), p. 7; (1900), pp. 14, 29, 99.
*G. fuscum*, Zacharias (1895), p. 134; (1896), pp. 37, 38, 51; (1896), p. 78; (1898*a*), p. 27; (1898*b*), p. 714; (1898*c*), pp. 95, 109; (1903), pp. 237, 244.
*G. fuscum*, Schütt (1895), p. 9; (1896), p. 5, fig. 5*a*. After Stein (1883).
*G. fuscum*, Entz (1896), p. 22.
*G. fuscum*, Apstein (1896), pp. 119, 120, 121, 131, 152, 153, fig. 53, tables 1–3.
*G. fuscum*, Lemmermann (1896), p. 94; (1900), p. 115; (1902), p. 260; (1903), pp. 118, 120, 123, 149; (1910), pp. 613, figs. 10, 11, pp. 618, 620. After Stein.
*G. fuscum*, Ludwig (1898), p. 5.
*G. fuscum*, Mez (1898), p. 216.
*G. fuscum*, Schröder (1898), p. 14.
*G. fuscum*, Iwanoff (1900), p. 140.
*G. fuscum*, Amberg (1900), p. 83.
*G. fuscum*, Huitfeldt-Kass (1900), p. 3.
*G. fuscum*, Lagerheim (1900), p. 22.
*G. fuscum*, Zschokke (1900), p. 345.
*G. fuscum*, Schönichen and Kalberlah (1900), p. 232, pl. 2, fig. 3; (1909), p. 252, pl. 8, fig. 3.
*G. fuscum*, Wesenberg-Lund (1904), pp. 106, 107, 112, tables 1–9.
*G. fuscum*, Bachmann (1907), p. 36.
*G. fuscum*, Karsten (1907), p. 466.
*G. fuscum*, Ostenfeld (1907), p. 390.
*G. fuscum*, Seligo (1907), p. 96, fig. 133.
*G. fuscum*, Doflein (1909), p. 521, fig. 462 A; (1911), p. 527, fig. 462 A.
*G. fuscum*, Senn (1911), p. 623.
*G. fuscum*, Francé (1912), p. 28.
*Peridinium fuscum*, Chatton (1912), p. 86.
*Gymnodinium fuscum*, Lauterborn (1913), p. 868.
*G. fuscum*, Cunha (1913), p. 105.

Diagnosis.—A medium sized species with ovoidal body, slightly flattened dorsoventrally, its length 1.5 transdiameters; girdle without displacement; sulcus extending from girdle to antapex; color yellow brown. Length, 88μ. In fresh-water swamps in central Europe.

Description.—The body is stout ovoidal, widest at the middle, slightly narrower posteriorly, its length about 1.5 transdiameters and its dorsoventral diameter 0.33 of its transdiameter. The epicone and hypocone are subequal. The epicone has a length of about 0.45 of the total length of the body. It is high dome-shaped with broad apex and symmetrically rounded sides. The hypocone is usually somewhat narrower than the epicone and tapers posteriorly to the pointed antapex.

The girdle is subequatorial in position and forms a complete circle around the body without displacement. The furrow is shallow and about 0.08 transdiameter in width with smooth borders. The sulcus begins at the girdle and extends posteriorly to the antapex in a straight line.

The nucleus is a small, spherical body near the anterior part of the epicone. Its diameter is about 0.2 transdiameter of the body in length. Numerous small, yellow brown chromatophores fill the peripheral zone of the cytoplasm.

Dimensions.—Length, 80–100$\mu$; transdiameter, about 58$\mu$; axis of nucleus, 12$\mu$.

Occurrence.—Described and figured by Ehrenberg (1834, date of separate publication) from fresh water in the vicinity of Berlin, May 4. Other records of its appearance are as follows: In Lake Plön, Germany, by Apstein (1896) in April-June, by Zacharias (1896), and by Lemmermann (1903) in March; by Stein (1883) near Chodau, Austria, and near Budapest, Hungary, by Entz (1896); by Wesenburg-Lund (1904) in all the Zealand and Jutland lakes in Denmark, from March to October; in Stor-Pentula Lake, Finland, by Levander (1900) in July; near Basel, Switzerland, by Schilling (1891), in Katzen Lake, Zurich, Switzerland, by Amberg (1900), and in Brazil by Cunha (1913).

Synonymy.—Described by Ehrenberg (1834) as *Peridinium fuscum,* the name was changed by Stein (1878) to *Gymnodinium fuscum.* It is the type species of the genus, being the first one named and figured by Stein.

Relationships.—This species belongs to the small group of fresh-water *Gymnodinium* characterized by the possession of yellow or yellow ochre chromatophores, and falls in the subgenus *Gymnodinium sensu strictu.* It is nearest related to *G. mirabile* in size and general proportions.

## **Gymnodinium fusus** Schütt

Text figure X, 5

*Gymnodinium fusus* Schütt (1895), pl. 24, fig. 79, pl. 25, fig. 81 (in part, pl. 25, fig. 81, is *Gyrodinium falcatum* sp. nov.); (1896), p. 5, fig. 5 D.

*G. fusus,* Karsten (1907), p. 340.

*G. fusus,* Entz, Jr. (1907), p. 11; (1909), p. 246.

*G. fusus,* Klebs (1912), p. 390.

*G. fusus,* Lemmermann (1910), p. 618.

Diagnosis.—Large sized species with spindle-shaped body, its length 2.06 transdiameters; girdle slightly premedian, its ends displaced its own width; sulcus extending from near the apex to the antapex; yellow-brown chromatophores. Length, 122$\mu$. Mediterranean or Atlantic, Arctic, Indian oceans.

Description.—The body is stout spindle-shaped, widest at the middle and tapering towards both ends, its length 2.06 transdiameters at the widest part. The hypocone exceeds the epicone in length by 0.15 of its own length. The epicone has a length on the left and right sides of about 0.39 and 0.44 respectively of the total length of the body. It is conical (45°) with sides irregularly sloping from the blunt apex to the girdle in ventral view. The hypocone is slightly broader (50°) and is less symmetrical. In lateral view the ventral side of the epicone is concave and of the hypocone convex, sloping abruptly to the narrow antapex.

The girdle is slightly premedian in position, meeting the sulcus proximally about 0.39 and distally 0.44 of the total length of the body from the apex. It traverses a slightly spiral course which displaces its distal end posteriorly about its own width. The furrow is deeply impressed and about 0.05 transdiameter in width. The sulcus begins a short distance below the apex and passes posteriorly to the antapex in an irregular course but with no torsion. It widens to about twice its own width posteriorly. No flagella or flagellar pores are noted by Schütt (1895).

The nucleus is ellipsoidal, and is located in the dorsal part of the hypocone. A coarse, chromatin network is figured by Schütt (1895, pl. 24, fig. $79_2$). Its major and minor axes are 0.47 and 0.40 transdiameter respectively. A number of oil droplets and food vacuoles are scattered through the cytoplasm, which is also filled with stout, rod-shaped, yellowish brown chromatophores.

Dimensions.—Length, 118–122μ; transdiameter, 58–59μ; dorsoventral diameter, 59μ; axes of nucleus, 27μ and 22μ.

Occurrence.—Figured by Schütt (1895) from the collections of the Plankton Expedition probably from the Mediterranean at Naples or from the Atlantic. The only other records are those of Karsten (1907) from the collection of the "Valdivia" Deep Sea Expedition, from the Indian Ocean, and Meunier (1910) from the Arctic near Spitzbergen.

Synonymy.—Schütt (1895) includes in this species two forms which appear to us to be generically separate. His figure 81, plate 25, with its girdle having a displacement of more than one-fifth (0.22) the length of the body, is generically distinct from his figure 79, plate 24, with its girdle displaced 0.06 the length of the body. The former falls within the genus *Gyrodinium* and to it we assign the new name *Gyrodinium falcatum*.

Comparisons.—Schütt (1895) figures no surface striae on this species. With its roughly fusiform body it is unique in the subgenus *Gymnodinium (sensu strictu)*, except for *G. filum* Lebour (1917*b*). Should striae be found on it the species should be transferred to the subgenus *Lineadinium*, composed of striate species, some of which, such as *G. cucumis* and *G. aureum*, are fusiform.

## **Gymnodinium gleba** Schütt

Text figure AA, 4

*Gymnodinium gleba* Schütt (1895), pl. 25, fig. 86; (1899), p. 629.
*G. gleba*, Lemmermann (1899), p. 358.

Diagnosis.—A large species with ellipsoidal body, its length 1.57 transdiameter; girdle displaced its own width; sulcus extending from the apex to the antapex. Length, 126μ. Atlantic or Mediterranean; Pacific off La Jolla, California.

Description.—The body is stout ellipsoidal, widest at the middle, its length 1.57 transdiameter at the widest part at the girdle. The epicone has a length at its left and right sides of 0.5 and 0.55 respectively of the total length of the body, exceeding the length of the hypocone by about 0.1 of its own length. It is symmetrically rounded with the apex forming a slightly rounded, blunt elevation. The hypocone is symmetrically rounded, bilobed at the antapex by the sulcal notch.

The girdle is somewhat submedian in position, meeting the sulcus proximally about 0.5 of the total length of the body from the apex and distally 0.55, being displaced about its own width. The furrow is wide, 0.06 transdiameter, and shallow. The flagellar pores and flagella were not noted by Schütt (1895).

The nucleus is ellipsoidal and is located near the antapex. It is filled with coarse, chromatin granules. Its major and minor axes are about 0.4 and 0.35 transdiameter respectively in length. The anterocentral part of the body is occupied by a large brownish mass, evidently a food body. The remainder of the body is filled with vacuoles of varying sizes. Color greenish grey. Scattered over the surface of Schütt's (1895) figure are small, blister-like projections. These were not observed in our specimen and are probably indicative of approaching cytolysis. No pusules were noted.

DIMENSIONS.—Length, 80–126μ; transdiameter, 59–80μ; axes of nucleus, 17–24μ by 28μ.

OCCURRENCE.—This was figured by Schütt (1895) from the collection of the Plankton Expedition from the Bay of Naples or from the Atlantic. A single specimen was taken 6 miles off La Jolla, California, July 1, 1906, in a haul from 995 meters to the surface. Unfortunately no color notes were made of this individual.

COMPARISONS.—Its thickened periplast, though lacking distinct ectoplasmic differentiation, places it in the subgenus *Pachydinium*, near *G. pachydermatum* (fig. AA, 5), but its girdle is more nearly submedian, its form less rotund, and it wholly lacks striae. The possession of an apical point is unusual in this subgenus.

## **Gymnodinium gracile** Bergh

Plate 2, figure 19; text figure Z, 3

*Gymnodinium gracile* Bergh (1881*b*), pp. 251–253, pl. 16, figs. 68, 69.
*G. gracile,* Entz, Sr. (1882), p. 189; Entz, Jr., as *Spirodinium gracile* (1902), p. 124; (1907), p. 17; (1909), p. 254.
*G. gracile,* Bütschli (1885), pp. 962, 964, 975, 1017, pl. 51, fig. 4.
*G. gracile,* Penard (1891), p. 59.
*G. gracile,* Schilling (1891), pp. 200, 206.
*G. gracile,* Lemmermann (1899), p. 358; (1902), p. 260.
*G. gracile,* Ostenfeld (1906), p. 6; (1913), pp. 123, 338, 344.
*G. gracile,* Paulsen (1907), p. 23; (1908), p. 98, fig. 133.
*G. gracile,* Wright (1907), p. 5, pl. 1, fig. 9.
Not *Gymnodinium gracile* Pouchet (1883, p. 446, pls. 20–21, fig. 39); (1885*a*, p. 97); Schütt (1887, pp. 373, 374); Fauré-Fremiet (1914, p. 42). These references all deal with Pouchet's figure and description, both of which leave his form indeterminable.

DIAGNOSIS.—A large species with long, subovoidal or ellipsoidal body, its length 2.1 transdiameters, epicone subconical; girdle premedian, displaced about twice its own width; sulcus extending from near apex to antapex; surface finely striate; color yellowish. Length, 105μ. Pacific off La Jolla, California, July, August; Baltic and Mediterranean seas, Cattegat, Atlantic.

Description.—The body is subovoidal to fusiform ellipsoidal in shape, circular in cross-section, its length 2.1 transdiameters at the widest part at the girdle. The hypocone exceeds the epicone in length by about 0.25 of its own length. The epicone is dome-shaped or subconical (50°–55°), flaring slightly at the base and broadly rounded at the apex. It has a length on the left and right sides of 0.37 and 0.44 respectively of the total length of the body. The hypocone is subcylindrical, flaring slightly at the girdle, and broadly rounded at the antapex, which is sometimes notched by the distal end of the sulcus. In lateral view the hypocone has an almost straight outline on the ventral side and convex on the dorsal.

The girdle is premedian, its proximal end meeting the sulcus at a distance from the apex of 0.37 and its distal end 0.44 of the total length of the body. It occupies a narrow, deep trough with smooth overhanging borders. Its distal end is displaced posteriorly about twice its own width. The sulcus begins near the apex or somewhat below it and extends posteriorly in an almost straight line to the antapex. It lies in a trough which is narrow anteriorly and widens posteriorly, forming a broad channel along the ventral face of the hypocone, the furrow itself remaining nearly the same width throughout. The anterior flagellar pore opens at the proximal junction of the girdle and sulcus and the posterior pore midway between the distal junction and the antapex.

The nucleus is an ellipsoidal body found in the posterior half of the hypocone. Fine, moniliform chromatin strands follow its longitudinal axis. Its major and minor axes are 0.54 and 0.46 transdiameters respectively in length.

Small sacklike pusules are usually present, opening into one or both pores. In one individual the pusule was large, subspherical and located near the center of the body. From it a long narrow canal passed to the anterior pore. The cytoplasm is finely granular and generally has many cell inclusions. In the apical region of one individual were a group of vacuoles filled with the pink fluid associated with the pusules. Just above the large pusule which occupied the center of the body was a group of dark, refractive granules from which extend radial, greenish rodlets of two sizes, long slender ones and short, thicker, more numerous ones. A small orange-colored body, presumably a food body, was found near the girdle. The ectoplasm shows the same differentiation into a thin layer surmountd by an alveolar layer as has been described for *G. dogieli* and *G. amphora*.

The color of the protoplasm is a pale, yellowish grey, but the color may vary considerably with different individuals. In some specimens observed the color was a yellowish brown with a large, orange red food mass in the epicone. In figure 19, plate 2, the color varies from bluish green in the apical region to yellow-green in the antapical region.

Dimensions.—Length, 105–130μ; transdiameter, 50–61μ; axis of nucleus, 25–30μ.

Occurrence.—The first specimens were taken July 16, 1907, in a surface haul 1 mile off La Jolla, California. On July 23 of the same season it was taken 0.75 of a mile off La Jolla in a surface haul. It was taken again on June 29, 1917, with a No. 12 silk net in a haul 1 mile off La Jolla, from 40 meters to the surface and in a surface temperature of 21°1 C. This species occurred abundantly throughout the summer in the surface hauls from the end of the pier and in the deeper hauls offshore. The number of individuals noted in a short examination of each haul would vary from 1 to 8 or more. The other and earlier records for this species are as follows: By Bergh (1881*b*), who first described it from the Baltic Sea; by Paulsen (1907), from the Cattegat off Denmark; by Wright (1907), from the Atlantic off Nova Scotia in July; by Ostenfeld (1913) from the Cattegat off the coast of Denmark.

SYNONYMY.—Originally described by Bergh (1881*b*) as *Gymnodinium gracile*. It was referred, without explanation, to *Spirodinium* by Entz, Jr. (1902, 1907, 1909), but the structure of the girdle, with little displacement and no overhang, does not justify the transfer. It stands near *Spirodinium*, however. Bergh's form was slightly smaller than the forms present at La Jolla, his measurements being 90μ long and 24μ wide. Pouchet (1883, 1885*a*) describes two forms as *G. gracile* Bergh which have no resemblance to each other and less to Bergh's figures (1881*b*). His earlier one (1883) shows a *Gymnodinium* without striae and the girdle slightly posterior to the midregion of the body. His second one (1885*a*) is a *Gyrodinium* with the girdle premedian and displaced 0.33 of the body.

The form described by Wright (1907) as *G. gracile* from the cold waters off the shores of Nova Scotia may be a doubtful member of this species. Much more work on these forms will be required before we can say, definitely, that these frail organisms can exist, as specifically identical individuals, in the warm waters of the Mediterranean and off the coast of the southern part of California, and in the cold waters of the Arctic current that bathes the eastern shores of Canadian America. His form also lacks the striate surface characteristic of *G. gracile*, but this may have been omitted in the drawing.

COMPARISONS.—This species belongs in the subgenus *Pachydinium* and finds its nearest counterpart in *G. abbreviatum* sp. nov. (fig. Z, 7), differing from it, however, in its lack of a distinct alveolar layer. It is somewhat like *G. aureum* sp. nov. (fig. Y, 3) in size and general proportions, but is of a duller color, more rotund hypotheca, different cell contents, and different striations.

## Gymnodinium gracile var. exiguum Pouchet

Text figure BB, 17

*Gymnodinium gracile* var. *exiguum* Pouchet (1883), p. 447, pls. 20, 21, fig. 40.
*G. gracile* var. *exiguum*, Lemmermann (1899), p. 358.
*G. gracile* var. *exiguum*, Paulsen (1908), p. 108.

DESCRIPTION.—An organism with a rotund body divided into two subequal parts by the girdle, slightly wider anteriorly. The complete course of the girdle and the sulcus are not figured or described by Pouchet (1883). The nucleus is a small, spheroidal body near the antapex. Near the nucleus is a large, irregular body of red pigment. The color of the organism is pale rose. Its length is 30μ, its transdiameter 15μ. Abundant in the Atlantic off Concarneau, France.

Pouchet's (1883) description and figure do not afford sufficient data for specific determination, or even generic status. The girdle on the dorsal side might be that of *Gyrodinium*. Until it has been redescribed it must, therefore, be placed among the species *incertae sedis*.

**Gymnodinium grammaticum** (Pouchet) emend. Kofoid and Swezy

Text figure X, 22

*Gymnodinium punctatum* var. *grammaticum* Pouchet (1887), p. 107, pl. 10, figs. 8–9.
*G. punctatum* var. *grammaticum*, Lemmermann (1899), p. 359.
*G. punctatum* var. *grammaticum*, Schröder (1900), p. 13.

DIAGNOSIS.—A minute species with rotund body, its length and transdiameter subequal; girdle median, without displacement; sulcus on hypocone only; very long red pigment spot on ventral face of hypocone in sulcus; color yellow. Length, 25μ. Atlantic off Concarneau, France, September; Gulf of Naples, July, August.

DESCRIPTION.—The body is irregularly rotund, somewhat asymmetrical, rounded anteriorly, notched posteriorly, its length and widest transdiameter subequal. The epicone and hypocone are subequal in length, but the hypocone contracts less than the epicone. The epicone is hemispherical in shape, flaring slightly posteriorly. Its length is about 0.5 of the total length of the body. The hypocone is rounded laterally with the antapex broadly notched by the distal end of the sulcus. The right side is slightly longer than the left.

The girdle is submedian in position. Its distance from the apex is about 0.5 of the total length of the body. It forms a complete circle around the body, the ends meeting the sulcus without displacement. The proximal lip is deeply undercut by the furrow. The sulcus is not well defined in Pouchet's figures (1887), but evidently extends at least from the girdle to the antapex.

The interior of the body is filled with small spherules. The nucleus was not noted by Pouchet. An elongated red pigment spot of exceptional size extends from the girdle to the antapex in the sulcal region of the ventral surface. The general color of the cytoplasm is yellow.

DIMENSIONS.—Length, 25–26μ; transdiameter, 23μ.

OCCURRENCE.—Figured by Pouchet (1887) from collections made in the Atlantic near Concarneau, France, in September. The only other record of its appearance is that of Schröder (1900) from the Gulf of Naples in July and August.

COMPARISONS.—A colored pigment spot of the type found in this species is rare among marine *Gymnodinium*, though rather common among fresh-water species. It belongs in the subgenus *Gymnodinium*.

## CHAPTER XII

# GYMNODINIIDAE: GYMNODINIUM (*continued*), G. HAMULUS TO G. ZACHARIASI

### **Gymnodinium hamulus** sp. nov.

Plate 9, figure 97; text figure Y, 5

Diagnosis.—A minute species with discoidal dorsoventrally compressed body, its length and transdiameter subequal; girdle submedian, without displacement; sulcus extending from girdle to antapex; surface striate; color green. Length, 16.5μ. Sand beach at La Jolla, California, July.

Description.—The body is discoidal, rotund in ventral view and dorsoventrally flattened, its dorsoventral diameter 0.61 of its transdiameter and its length and transdiameter subequal. In lateral view the dorsal surface is more convex than the ventral. The epicone and the hypocone are subequal. The epicone is semicircular in shape in ventral view with the short pointed apex sharply deflected to the left and dorsad. Its greatest length is 0.5 of the total length of the body. The hypocone is slightly broader than the epicone, with rounded sides and antapex broadly notched by the distal end of the sulcus. In lateral view the ventral side shows a slight sigmoid curve in its surface with the dorsal side convex.

The girdle is submedian in position, its greatest distance from the apex being 0.5 of the total length of the body. It forms a complete circle around the body with a slight deflection posteriorly on the ventral face at its junction with the sulcus. The furrow is wide, about 0.11 transdiameters, and rather deeply impressed with smooth borders. The sulcus is wider than the girdle, expanding to nearly twice its width anteriorly at the junction with the girdle and slightly more posteriorly, where the borders are widely deflected and extend around to the dorsal surface, forming a deep sulcal notch at the antapex. The anterior flagellar pore is found at the union of the two ends of the girdle, the posterior pore about one width of the girdle posteriorly.

The nucleus is spherical and is located slightly posterior to the central part of the body. Its axis is about 0.27 transdiameter in length.

The cytoplasm is clear and contains numerous blue-green spherules. The surface is striate with blue-green striae, which are equidistant and parallel throughout their length, and about twenty in number across the ventral face and equal in number on epicone and hypocone. The general color of the organism is blue green. In many individuals a small red-brown mass, probably a food body, is found in the epicone.

Dimensions.—Length, 16.5μ; transdiameter, 16μ; dorsoventral diameter, about 7μ; axis of nucleus, 5μ.

Occurrence.—This species was found very abundantly in the beach sands at La Jolla, California, in July, 1914. On August 13 and 15, 1917, several individuals were observed in the hauls made 0.75 mile offshore from 83 meters and 70 meters to the surface respectively.

Comparisons.—This is one of the smallest of the Gymnodiniidae, a single species, the fresh-water *G. varians*, 11μ in length, being smaller. It is typically a sand-beach form, and shows, in the dorsoventral compression of the body, a

characteristic of *Amphidinium,* one of its associates in that habitat. It was found in company with *Amphidinium scissum, A. truncatum, A. corpulentum,* and *A. asymmetricum.* It belongs in the subgenus *Lineadinium,* but is wholly unlike any other species. The apical hook is homologous with that found in *G. vestifici,* but there are wide differences in the proportions of the body between these two species. In form, proportions, and apical hook it is close to *G. agile* sp. nov. (fig. Y, 9), but this species is larger, lacks striae, and has chromatophores.

## Gymnodinium helveticum Penard

Text figure Y, 11

*Gymnodinium helveticum* Penard (1891), pp. 6, 21, 22, 47, 58, 59, pl. 5, figs. 10–16.
*G. helveticum,* Imhof (1892), p. 175.
*G. helveticum,* Lemmermann (1900), p. 116; (1902), p. 260; (1910), pp. 613, 618, 619, 621, figs. 17–19.
*G. helveticum,* Lauterborn (1910), p. 471; (1913), pp. 864, 902, 906.
*G. helveticum,* Schilling (1913), p. 20, fig. 20.
*G. helveticum,* West (1916), p. 53.

Diagnosis.—A small species with subovoidal body, its length 1.66 transdiameters; girdle premedian, displaced its own width; sulcus invading both epicone and hypocone; surface striate; color, rose. Length, 50μ. Lake Geneva, Switzerland, Rhine River, Germany.

Description.—The body is symmetrically subovoidal, widest anteriorly at the girdle, tapering posteriorly, its length 1.66 transdiameters at the widest part. The epicone is shorter than the hypocone by about 0.37 of its length. It is subconical, about 70°, with rotund sides. The apex is acuminate-truncate with three minute, pointed projections, the middle one being about twice the height of the other two. The epicone has a length on the left and right sides of 0.36 and 0.4 respectively of the total length of the body. The hypocone is conical, about 55°, with a slender, acuminate antapex.

The girdle is premedian in position, its proximal end joining the sulcus at a distance from the apex of 0.36 and its distal end 0.4 of the total length of the body. The furrow is wide, about 0.1 transdiameter, its proximal end about half that width and its distal end almost obscured by the overhanging proximal border. Its depth is about 0.3 radius and its sides form an obtuse angle with the surface of the hypocone and an acute one with the surface of the epicone. The sulcus begins just below the apex and extends posteriorly in an almost straight line to within a short distance of the antapex. Its borders in the posterior part are drawn out into two pointed flaps, the one on the right side much nearer the antapex than the one on the left. The longitudinal flagellum arises at the junction of the girdle and sulcus. The transverse flagellum was not observed by Penard (1891).

The nucleus is an ellipsoidal body found in the middle of the body in the region of the union of girdle and sulcus. Its long axis is parallel with the long axis of the body. It is filled with coarse, chromatin strands lying parallel with its major axis. Its major and minor axes are about 0.53 and 0.28 transdiameter respectively in length.

The cytoplasm is clear, with numerous refractive granules in the peripheral zone. The general color of the organism is the rose color of the peach blossom. A small spherical pusule is found immediately behind the point of union of girdle and sulcus. The surface is covered

by fine striae, longitudinally arranged, about 15 across the ventral face, equal in number on epicone and hypocone, with fine, colorless granules strung along them like beads on a string. Nutrition is holozoic.

Dimensions.—Length, 50μ; transdiameter, 30μ; axes of nucleus, 16μ and 8.5μ.

Occurrence.—This was figured by Penard (1891) from Lake Geneva, Switzerland. The only other record of its occurrence is that of Lauterborn (1910) from the Rhine River near Neuhofen, Germany.

Comparisons.—This species greatly resembles *G. aureum*, a marine form found in the Pacific at La Jolla, California, and is probably its fresh-water representative. The latter is larger with slightly different proportions. The differences might easily be accounted for by the change of habitat. It belongs to the subgenus *Lineadinium*, but has no other close relations therein.

## **Gymnodinium herbaceum** Kofoid MSS.

Plate 4, figure 44; text figure Y, 17

Diagnosis.—A small species with ovoidal body, its length 1.54 transdiameters: girdle displaced its own width; sulcus extends from girdle to near the antapex; surface on hypocone striate; chromatophores green. Length, 55μ. Mediterranean at Naples, January.

Description.—The body is ovoidal, circular in cross-section, very slightly wider anteriorly with its length 1.54 transdiameters at the widest point. The epicone is exceeded in length by the hypocone by 0.36 of the length of the latter. Its lengths at the proximal and distal ends of the girdle are 0.36 and 0.43 respectively of the total length of the body. The apex is rounded, subhemispherical. The hypocone has a length on the left and right sides of the sulcus of 0.58 and 0.50 respectively of the total length of the body. The antapex is broadly rounded with no sulcal notch.

The girdle is preëquatorial in position and follows a slightly spiral course in which its distal end becomes displaced posteriorly about its own width. Its anterior and posterior junctions with the sulcus occur at 0.36 and 0.43 respectively of the total length from the anterior end. It occupies a furrow about 0.1 transdiameter in width which is lightly impressed with prominent lips. The sulcus extends from its anterior junction with the girdle to near the antapex in a straight line. The anterior flagellar pore opens at the anterior junction and the posterior pore slightly below the posterior junction of the girdle and sulcus. The transverse flagellum is about 0.5 of the length of the girdle and the longitudinal one about 1.5 lengths of the body in length.

The nucleus is a small, spheroidal body lying in the posterior half of the body. Its axis is about 0.3 transdiameter in length. Coarse, moniliform chromatin strands follow a spiral course about its longitudinal axis. No pusules were noted. In the central part of the epicone was a large, spheroidal, fluid-filled vacuole, pale turtle green in color. Crowded about these were numerous smaller vacuoles, green and blue in color. In the peripheral zone were numerous minute, highly refractive, blue-green spherules and irregularly shaped, disklike green chromatophores. The surface of the hypocone is striate with blue-green striae, about ten on a hemisphere. These fade out before reaching the girdle or the antapex. None could be detected on the epicone.

Dimensions.—Length, 55μ; transdiameter, 35μ; axis of nucleus, 11μ.

Occurrence.—Several individuals observed in the plankton of the Bay of Naples, on January 23, 1908, by the senior author.

COMPARISONS.—This species comes closest in its general size and proportions to *G. ravenescens*. It differs from it, however, in its striate surface and in its chromatophores. That it is holozoic in nutrition might be inferred from the number and size of fluid-filled vacuoles present. In this respect it recalls the conditions figured by Stein (1883, pl. 17, figs. 14-16) for *Amphidinium steini*. This species possesses chromatophores, yet is capable of ingesting smaller organisms (*G. ravenescens* and *G. flavescens* also exhibit indications of holozoic nutrition). It belongs to the subgenus *Gymnodinium*, but in the presence of few striae on its surface it inclines towards the next subgenus, *Lineadinium*. Chromatophores are relatively rare in the subgenus *Gymnodinium*, being possessed by only a few small forms, mostly fresh-water in habitat.

### **Gymnodinium heterostriatum** nom. sp. nov.

Plate 2, figure 24; plate 5, figure 56; text figure Y, 7

*Gymnodinium spirale* var. *obtusum* Dogiel (1906), pp. 38–43, pl. 2, figs. 50–56.
*G. spirale* var. *obtusum*, Entz, Jr. (1907), p. 17; (1909), p. 254.
*G. spirale* var. *obtusum*, Klebs (1912), p. 430.

DIAGNOSIS.—A medium sized species with symmetrical ellipsoidal body, its length 1.5 transdiameters; girdle submedian, displaced its own width; sulcus extending from apex to antapex; surface heterostriate; color pinkish cinnamon. Length, 67μ. Pacific off La Jolla, California, June to August; Gulf of Naples, May to July.

DESCRIPTION.—The body is of robust habit, varying in shape from broadly ellipsoidal to biconical or ovoidal with broadly rounded apices, its length about 1.5 transdiameters. It is nearly circular in cross-section. The epicone and hypocone are subequal. The epicone is broadly dome-shaped with broad, rounded apex. It has a length on the left and right sides of about 0.52 and 0.59 respectively of the total length of the body.. The hypocone is subconical, about 50°, with rounded sides and blunt apex. It is usually slightly less in transdiameter than the epicone, with narrower antapex.

The girdle is submedian, its proximal end joining the sulcus at a distance from the apex of 0.52 of the total length of the body. It forms a descending left spiral, its distal end joining the sulcus at a distance from the apex of 0.59 of the total length of the body, being displaced about its own width accompanied by a slight overlapping. It usually exhibits a slight sigmoid curve at its proximal end, in the lower curve of which opens the anterior flagellar pore. The furrow is wide, about 0.08 transdiameter, and deeply impressed, its upper lip slightly raised and cut under almost horizontally, while the lower one is more gradually curved. The borders are marked by a double-contoured line usually blue green in color. The sulcus is very narrow and extends in a sinuous line from the apex to the antapex. It becomes very shallow on the hypocone and fades away near the antapex. The posterior flagellar pore is found a short distance posterior to the distal junction of the girdle and sulcus.

The nucleus lies slightly anterior to the center and somewhat to the right side. It is nearly circular in outline. In one individual under observation the circular nucleus changed after about 40 minutes to a reniform shape with a distinct hollowing out, the concavity being occupied by a granular body recalling the dumbbell-shaped centrosphere or paradesmose of *Noctiluca* (Ishikawa, 1894, Calkins, 1901, and Doflein, 1911). Mitosis was not accomplished prior to dissolution. The axis of the nucleus is about 0.43 transdiameter in length.

A small sacklike pusule is usually present, opening into the anterior flagellar pore. The cytoplasm is granular and generally shows numerous cell inclusions. These include minute spheroidal oil droplets in the peripheral zone, a dense layer of short blue-green rodlets perpendicular to the surface, large pinkish vacuoles and food bodies. This species showed more remarkable cannibalistic habits than any other species of the Gymnodiniidae which we examined. Many specimens were met in which the body had been greatly enlarged, sometimes twice the normal size, by the ingestion of other unarmored dinoflagellates. These would often continue active until the water on the slide had partly evaporated, when the food mass would be ejected from the body by a posterior vent. The host would continue swimming about with the posterior vent in the body gradually folding and closing in until it became invisible. One encysted individual was noted which contained a large food mass, evidently the remains of a dinoflagellate.

The surface is covered with longitudinal equidistant striae, about 18 across the ventral face of the epicone. These are about twice as numerous on the hypocone as on the epicone. They may be composed of unbroken lines from the apices to the girdle or may be short, broken lines or granules linearly arranged, diminishing in number as they near the apices. Their color is blue green. Between the striae in surface view are seen the ends of the peripheral layer of short rodlets.

One individual when first observed was suffused at both poles (pl. 2, fig. 24) with a reddish brown tone, fading out centrally. This color, however, soon faded out, leaving no trace and no aggregated condensations of colored substances. In general the color is a mixture of pale chalcedony yellow and pinkish cinnamon diffused through the cytoplasm. Many individuals enclosed in thin-walled hyaline cysts were noted.

Dimensions.—Length, 66–85$\mu$; transdiameter, 48–72$\mu$; axes of nucleus, 22$\mu$ and 32$\mu$.

Occurrence.—This was figured by Dogiel (1906) from the Bay of Naples, May to July. The first appearance of this species in the Pacific was recorded July 19, 1906, from a haul made with a No. 20 silk net from 585 meters to the surface off La Jolla, California. During June, July, and August, 1917, this was present in most of the hauls made off La Jolla, including a few of the surface hauls at the end of the pier at the Biological Station. The number of individuals noted in a short examination of a single haul varied from 1 to 10. It was the most abundant species of the Gymnodinioidae in plankton examined by us.

Comparisons.—The food habits of this minute form make it one of the most interesting species in the genus. In the many individuals seen practically none was without ingested food masses. It is more sensitive to the adverse conditions found under the microscope than most of the other species, in that the food masses were usually disgorged shortly after being placed under observation. This may have been caused by contact with the cover glass or by the intense illumination required for the microscope. In its abundance of peripheral rodlets it resembles *Gyrodinium fissum* and, less strikingly, *Gymnodinium doma*. It belongs to the subgenus *Lineadinium* and appears to be unique in the well defined and seemingly general contrast in the number of striae on the epicone and hypocone. A slight excess on the hypocone appears also in *G. rubrum* (fig. Y, 4) and in *G. multistriatum* (fig. Y, 1).

Synonymy.—Dogiel (1906) described, as *Gymnodinium spirale* var. *obtusum* Schütt, a form identical with our species. Schütt's organism (1895) of that name, however, is a *Gyrodinium*, and not the same as Dogiel's form. We therefore place the latter with our species as *Gymnodinium heterostriatum* nom. sp. nov.

## **Gymnodinium incisum** sp. nov.

Plate 3, figure 27; text figure X, 33

Diagnosis.—A small species with rotund body, its length and transdiameter equal; girdle a submedian, descending left spiral, displaced 0.19 transdiameter; sulcus extending from near apex to antapex; color, oil yellow. Length, 52μ. Pacific off La Jolla, California, August.

Description.—The body is rotund, rounded anteriorly, deeply notched posteriorly, its length equal to its widest transdiameter. The epicone and hypocone are subequal, their greatest lengths being the same. The epicone is hemispherical in outline with a slight irregularity in its contour at the apex, tending towards the formation of a low point or peak. The sides are smoothly rounded. In cross-section the shape is nearly circular with only a slight flattening on the midventral surface. It has a length on the left and right sides of 0.34 and 0.55 respectively of the total length of the body. The hypocone has more steeply sloping sides than the epicone and its greatest transdiameter is slightly less. The antapex is narrower than the apex, its sides smoothly rounded with a deep central excavation formed by the distal end of the sulcus. This produces two lobes in ventral view, each having a length of about 0.09 of the total length of the body. Anteriorly the sides of the hypocone flare out in a broad shelflike border to the girdle.

The girdle is slightly premedian in position for the greater part of its length. Its proximal end joins the sulcus at a distance from the apex of 0.34 and its distal end at 0.55 of the total length of the body. Its course is that of a descending left spiral with the distal end displaced posteriorly 0.19 transdiameter. The furrow is wide, about 0.05 transdiameter, and is deeply impressed. Its borders are raised slightly above the surrounding surface of the body.

The sulcus invades the epicone as a shallow trough which is deflected to the right at an angle of about 42° with the median longitudinal plane of the body. It fades out when slightly more than midway of the distance from girdle to apex. After meeting the proximal end of the girdle it turns and passes in a nearly straight line to the antapex. The trough widens at the anterior pore and deepens posteriorly until, in the antapical region, its depth becomes equal to the dorsoventral diameter at that plane. It cuts the dorsal surface of the body, forming two lateral lobes separated by a deep excavation at the antapex. The anterior pore opens at the proximal junction of the girdle and sulcus, the posterior pore about midway between the distal junction and the antapex.

The nucleus is a large body, ellipsoidal with slightly concave sides. It is found in the left anterior part of the body with its long axis diagonal to the long axis of the body. It is filled with coarse chromatin strands. Its major and minor axes are about 0.57 and 0.34 transdiameter respectively in length.

A small sacklike pusule opens into each flagellar pore. The cytoplasm is finely granular and contains an abundance of minute green oil droplets scattered through the peripheral zone. Nutrition is holozoic, as indicated by the presence in the body of an ingested *Pouchetia*, probably *P. rubescens*. This had been partly digested, its Indian-red color still noticeable and its ocellus conspicuous. The general color of the organism is oil yellow with a pearl grey background, the general effect quite rich.

DIMENSIONS.—Length, 52μ; transdiameter, 52μ; axes of nucleus, 30μ and 18μ.

OCCURRENCE.—One individual was taken August 21, 1917, with a No. 25 silk net, 5 miles off La Jolla, California, in a haul from 85 meters to the surface.

COMPARISONS.—In size, shape, proportions, and sulcal notch this species is very similar to *G. sulcatum* sp. nov. (fig. X, 1), but differs from it in the entire absence of the rose red color and of the scattered striae on the hypocone. Its sulcus is oblique and its girdle is rather widely displaced, while that of *G. sulcatum* is without displacement.

### **Gymnodinium inerme** (Schmarda) Saville-Kent

Text figure BB, 15

*Peridinium inerme* Schmarde (1854), p. 10, pl. 1, fig. 8.
*Gymnodinium inerme,* Saville-Kent (1880–82), p. 444, pl. 25, fig. 54.

DESCRIPTION.—A minute species with ellipsoidal body, its length 1.14 transdiameters. The epicone and hypocone are equal in size with the girdle occupying the midplane of the body. No sulcal notch. The color is red. Length, 16μ. Egypt, March, in fresh water.

SYNONYMY.—This minute form was figured by Schmarda (1854) as *Peridinium inerme* and the name changed by Saville-Kent (1880–82) to *Gymnodinium inerme*. Schmarda's figures lack nucleus, sulcus and the location of the girdle on the ventral face of the organism, i.e., it lacks sufficient morphological characteristics to establish it as a valid species. It is, therefore, placed among the species *incertae sedis.*

### **Gymnodinium lachmanni** Saville-Kent

Text figures BB, 4, 6

*Peridinium* sp. Claparède and Lachmann (1858–61), pp. 71, 73, pl. 13, figs. 21, 22.
*Gymnodinium lachmanni,* Saville-Kent (1880–82), p. 444, pl. 25, figs. 58, 59.

Saville-Kent (1880–82) has given this name to two forms figured as two different, unnamed species of *Peridinium* from the coast of Norway by Claparède and Lachmann (1858–61). The two organisms differ greatly from each other, with no indications of near relationship. They, likewise, may be, in part (our fig. B, 4), *Peridinium* which have escaped from the shells, as sometimes happens, or they may be *Gymnodinium.* Until they have been rediscovered, however, they must be placed among the species *incertae sedis.* The one (our fig. BB, 4) appears to be a rounding-up individual of a species near *G. marinum* Saville-Kent, approaching cytolysis, and the other might be an obliquely lateral view of a small individual of our own species, *G. dogieli* (fig. Z, 1, 2), assuming that Claparède and Lachmann have given correct magnifications of their figure.

## **Gymnodinium lineatum** sp. nov.

Plate 1, figure 2; text figure Y, 14

Diagnosis.—Large species with ovoidal body, its length 1.7 transdiameters; girdle submedian in position, displaced 0.2 transdiameter; sulcus extending from the apex to the antapex; surface striate; color, pale green yellow. Length, 143$\mu$. Pacific off La Jolla, California, July.

Description.—This is one of the largest species of *Gymnodinium*. The body is ovoidal, rounded at both apices, widest anteriorly, its length 1.7 transdiameters at the widest part. A cross-section of the body is nearly circular. The epicone, having a greater width than the hypocone, is slightly larger, though it is exceeded in length by the hypocone by 0.1 of its length. The epicone is irregularly, somewhat asymmetrically rounded with broad apex. It has a length on the left and right sides of 0.38 and 0.49 respectively of the total length of the body. The hypocone is much narrower than the epicone, conical in shape, about 50°, the angle increasing slightly near the girdle, with a broad, blunt antapex. Anteriorly it flares out in a wide, shelflike border to the girdle.

The girdle is submedian in position. Its proximal end joins the sulcus at a distance from the apex of 0.38 of the total length of the body. It follows a descending left spiral course around the body and its distal end meets the sulcus at a distance from the apex of 0.49 of the total length of the body, giving it a displacement of 0.2 transdiameter, or about 3 times its own width. The furrow is wide, about 0.05 transdiameter, and deeply impressed with wide, overhanging shelflike borders. The sulcus begins at the apex and extends posteriorly as a shallow channel. It follows a slightly sinuous course which is deflected to the left posterior to the proximal junction with the girdle, terminating near the left side of the antapex. The anterior flagellar pore is found at the proximal junction of the girdle and sulcus. The posterior pore is about a width of the girdle below the distal junction.

The cell inclusions consist of nucleus, pusule, vacuoles, small spherules and rose-red coloring material. The nucleus is a large ellipsoidal body in the left central part of the epicone. It is filled with fine, moniliform chromatin strands arranged along its shorter axis. Its major and minor axes are about 0.47 and 0.3 transdiameter respectively in length.

A large pusule opens into the anterior flagellar pore. It has an irregular sacklike extension anteriorly and a larger one posteriorly, both branches joining immediately dorsad of the anterior pore. No pusule could be detected in the region of the posterior pore. The cytoplasm is coarsely granular and alveolate in structure. Near the central part of the body is a mass of large, greyish vacuoles and scattered sparsely through the remainder of the body are smaller vacuoles filled with the same salmon-pink fluid found in the pusules. The general color of the organism is a pale green yellow diffused through the body.

The surface is marked by equidistant striae, about 25 across the ventral face. These consist of linear series of minute, rod-shaped, blue-green, lenticular bodies. The number is approximately the same on both epicone and hypocone. On the epicone these extend from girdle to apex, diminishing in number as they near the apex. On the hypocone they are deflected posterosinistrally, following the border of the sulcus on the left side but having a greater obliquity on the right, where they extend from the girdle to the right border of the sulcus.

Dimensions.—Length, 112–143$\mu$; transdiameter, 68$\mu$; axes of nucleus, 34$\mu$ and 23$\mu$.

Occurrence.—The first specimen observed was taken July 14, 1906, with a No. 20 net in a surface haul 2 miles off La Jolla, California. The individual figured was taken July 26, 1917, with a No. 25 net, 2.5 miles off La Jolla, in a

haul from 80 meters to the surface and in a surface temperature of 22°2 C. The same species was noted July 27, 4 miles off La Jolla, in a surface haul with a surface temperature of 21°9 C.

Comparisons.—This form is unique among the Gymnodiniidae in having its surface striae extending in an oblique rather than a longitudinal direction. This is apparently not the result of any torsion of the body. In forms having a greater torsion of the body, as *Gyrodinium* and *Cochlodinium*, the course of the surface striae, where such are present, is invariably longitudinal, with only a slight tendency to follow the course of the sulcus on the left side. In *Gymnodinium lineatum* this tendency is greatly exaggerated until the striae on the right side of the body are cut off in their course by the sulcus. It belongs to the subgenus *Lineadinium*, close to *G. rubrum*, which it approaches in proportions and size as well as in color. Its surface markings are quite different and its nucleus lacks the clear zone of that in *G. rubrum*.

### **Gymnodinium lineopunicum** sp. nov.

Plate 6, figure 65; text figure X, 17

Diagnosis.—A medium sized species with broad, ovoidal body, its length 1.09 transdiameters; girdle forming a complete circle about the middle of the body; sulcus short on epicone and hypocone; color, pomegranate purple. Length, 78µ. Pacific off La Jolla, California, August.

Description.—The body is rotund, ovoidal, broad anteriorly, tapering posteriorly, circular in cross-section, its length 1.09 transdiameters at the widest part. The epicone is larger in extent than the hypocone. It is hemispherical with broad apex and symmetrically rounded sides. Its length is about 0.47 of the total length of the body. The hypocone has the shape of a cone of about 75°, with a broad base and a blunt antapex. Its sides are symmetrical and very slightly convex.

The girdle forms a complete circle about the middle of the body. Its distance from the apex is 0.47 of the total length of the body. The furrow is wide, about 0.04 transdiameter, and rather deeply impressed. The anterior border is undercut somewhat, the furrow gradually rounding out to the posterior border. The sulcus is a very short, deep trough at its junction with the girdle, soon fading out both anteriorly and posteriorly, its length on the hypocone being about twice that on the epicone. The anterior flagellar pore opens at the junction of girdle and sulcus. The posterior pore is about two widths of the girdle below the anterior one.

The nucleus is a small, broadly ellipsoidal body, placed slightly posterior to the central part of the hypocone. It is filled with coarse, moniliform, chromatin strands. Its major and minor axes are 0.3 and 0.21 transdiameter in length respectively.

A small sacklike pusule opens into each flagellar pore, the anterior one exceeding the posterior one in size. The cytoplasm is finely granular, clear and translucent. The individual under observation had ingested a *Pouchetia*, probably *P. rubrum*, which was in process of digestion. A trace of the girdle remained, with the nucleus and ocellus still intact. The rose color was still present but diffusing out through the surrounding cytoplasm of the devourer. Nutrition in this species is patently holozoic.

The most striking feature of this organism is its color, which makes it a conspicuous object when placed under the microscope. The background of translucent cytoplasm is a pale turtle

green. Standing out in relief against this is the pomegranate-purple coloring matter or pigment, located in the peripheral zone, immediately beneath the thin periplast. This is amoeboid in character and changes its shape and position so rapidly that it is impossible to obtain a complete camera drawing of its appearance at one time. On the epicone it is located in stout rods linearly arranged, on the hypocone in irregular masses held in a coarse network of the same material. The dorsal location of this color was only a temporary localization. When first observed it was spread over a greater portion of the body. The surface was free from striations or other markings, but the pigment localization on the epicone strongly suggests a fundamental tendency in the direction of the linear organization of subpellicular substance in parallel equidistant lines.

DIMENSIONS.—Length, 78$\mu$; transdiameter, 70$\mu$; axes of nucleus, 21$\mu$ and 15$\mu$.

OCCURRENCE.—This species was represented by a single individual in the material under observation. It was taken August 8, 1917, with a No. 25 net in a haul 4 miles off La Jolla, California, from 80 meters to the surface and in a surface temperature of 22°5 C.

COMPARISONS.—This is one of the most strikingly colored species of *Gymnodinium*. It is unique, also, in the extreme mobility of the "chromatophores," if one may so term the color masses. This mobility resembles the condition exhibited by the color masses in *Gyrodinium ochraceum* (pl. 7, figs. 76, 82), and, perhaps, in *Erythropsis scarlatina*. In the latter species, however, active movement of the pigment mass was not observed, but its appearance suggested the probability that it takes place. The striate arrangement of the color on the epicone and the total lack of such arrangement on the hypocone suggests a fundamental tendency towards striate organization in the cytoplasm of that region similar to that in *G. contractum*.

This species is unique in *Gymnodinium* in the proportions of epicone and hypocone, resulting in a balloon-shaped body, further marked off by its prominent purple color pattern. It is one of the most highly specialized and widely divergent types found in the subgenus *Gymnodinium*. The possibility that its hypocone may be modified in form by the recent discharge of a large food body, and that the color has been, in part at least, derived from, or modified by, the food previously digested is not precluded.

## **Gymnodinium lira** sp. nov.

Plate 3, figure 30; text figure Z, 11

DIAGNOSIS.—This is a large species with rotund, ellipsoidal body, its length 1.47 transdiameters; girdle premedian, displaced about twice its own width; sulcus, extending from apex to antapex; surface ribbed; color, grey green. Length, 103$\mu$. Pacific off La Jolla, California, June, September.

DESCRIPTION.—The body has a rotund habit, widest in the middle with broad, rounded apices, a cross-section nearly circular in outline, its length 1.47 transdiameters at the widest part. The hypocone exceeds the epicone in size, being longer by 0.26 of its own length. The epicone is dome-shaped, or convex conical, flaring slightly at the girdle, with broad rounded apex. The

right side is somewhat more convex than the left. It has a length on the left and right sides of 0.36 and 0.43 respectively of the total length of the body. The hypocone is constricted slightly a short distance beyond the girdle, expands in the posterior third and is rounded posteriorly, with broad, hemispherical antapex. In the region of the girdle it flares out to form a broad lip.

The girdle is premedian, its proximal junction with the sulcus occurring at a distance from the apex of 0.36 of the total length of the body. It turns posteriorly, at an angle of 25° with the transverse plane of the body, for a short distance, then passes almost transversely around the body with a slight anterior deflection. Its distal end makes a short, abrupt posterior turn, meeting the sulcus at an angle of 40° from the transverse plane of the body. The furrow is wide, about 0.05 transdiameter, and deeply impressed, its anterior lip undercut and its posterior one gradually rounded. Both borders are raised considerably above the surrounding surface of the body. The sulcus extends from the apex to the antapex in a slightly sinuous line. The trough is shallow and narrow with a slight widening at the junctions with the girdle, and fading out near both apices. The anterior flagellar pore opens at the proximal junction of girdle and sulcus, the posterior pore at the distal junction.

The nucleus is ellipsoidal and is found in the anterior part of the body. It is filled with coarse chromatin strands. Its major and minor axes are about 0.32 and 0.27 transdiameter in length respectively.

The protoplasm is finely granular, grey green in color, and contains many large, pinkish vacuoles. Distinct alveoli are sometimes found in the peripheral zone (fig. Z, 11). The centro-posterior part of the body is filled with a large, irregular body, pale pink in color, containing a smaller yellow-green body near its center. This indicates a holozoic type of nutrition. Pusules were not in evidence in the individual studied.

A distinct pellicle is present of slightly greater consistency than most of these organisms possess. This is shown in the fact that it is occasionally found in preserved material with body intact, the only recognizable *Gymnodinium* we have met in our examination of several hundred plankton catches made at La Jolla and preserved in formalin. The surface is covered with longitudinal, equidistant ribs, yellow green in color, which are raised slightly above the surface near the middle of the body, gradually sinking and continuing as surface lines to the apices. It may also present high ridges on the surface. The girdle is outlined with lines of the same yellow-green color.

Dimensions.—Length, 103μ; transdiameter, 70μ; axes of nucleus, 23μ and 19μ.

Occurrence.—One individual was taken June 12, 1917, from a surface haul at the end of the pier at the Biological Station at La Jolla, California. It was also found in material preserved in formalin that had been collected September 24, 1904, 10 miles off La Jolla, in a surface haul with a No. 20 silk net.

Comparisons.—Although showing no differentiated ectoplasm of quite the same type as *G. dogieli* and *G. pachydermatum* (figs. AA, 1, 5), yet its thickened periplast places it in the same group with them. In the presence of distinct ribs on the surface, as distinguished from striae or furrows, it stands almost alone in *Gymnodinium*, *G. sulcatum* alone showing a few ridges on the hypocone. *Amphidinium fastigium* exhibits the same type of surface markings, though the ridges are fewer in number.

### **Gymnodinium lohmanni** Paulsen

Text figures BB, 1, 5, 12

*Gymnodinium roseum* Lohmann (1908), pp. 202, 252, 263–264, 366, 368, pl. 17, figs. 24–28; (1911), p. 20.

*G. lohmanni* Paulsen (1908), pp. 99–100, fig. 137 A–D.

*G. lohmanni,* Ostenfeld (1913), p. 338.

Not *G. roseum* Dogiel (1906), pp. 21–26, pl. 2, figs. 26–37, now *Chytriodinium roseum* (Dogiel) Chatton (1912).

In 1908 Lohmann published a description and four figures of a species which he called *Gymnodinium roseum.* It is a large species 70–115μ long, with rotund ovoidal body, asymmetrical, non-terminal horn, premidian transverse girdle, rounded antapex. The sulcus was not found. In his figure 26 it appears that the girdle is oblique, as in *Gyrodinium*, but this is based on preserved material, and may be distorted or even another species, perhaps of *Gyrodinium.* Its apex, however, is of the *G. lohmanni* type. It is probable that the asymmetrical spiral horn is related to our apical loop of the sulcus.

The cytoplasm is filled with stout, rodlike, peripheral rhabdosomes in radial or longitudinal arrangement and crowded with large vacuoles filled with a rosy fluid. An ellipsoidal nucleus, with spirally arranged parallel chromatin threads, is variously located within the cytoplasm, which also contains what appear to be food balls of various sizes. It is evidently a holozoic species.

While its girdle is indicated, its sulcus is not delineated, hence it is impossible to define its relationships with certainty, even as to its generic allocation. We therefore leave it tentatively in *Gymnodinium.*

SYNONYMY.—Lohmann (1908) described it as *Gymnodinium roseum,* using a name preoccupied by *G. roseum* of Dogiel (1906), a species which was later transferred by Chatton (1912) to his parasitic genus *Chytriodinium.* Paulsen (1908), in his monograph of the Peridiniales in "Nordisches Plankton," recognized the error of Lohmann and gave the species the name *G. lohmanni.*

### **Gymnodinium lunula** Schütt

Plate 5, figure 55; text figure I

"*Kystes des Péridiniens*" Claparède and Lachmann (1858–61), pp. 69–73, pl. 13, figs. 16–22.

*Gymnodinium lunula* Schütt (1895), in part, pp. 4, 11, 43, pl. 24, figs. $80_{+2,\,-5,\,-12,\,-14}$, pl. 25, figs. $80_{+3,\,-4,\,-6,\,-7,\,-11,\,-13}$; as *Pyrocystis lunula* (1896), pp. 3, 4, figs. 2 B–F.

*Pyrocystis lunula,* Jörgensen (1899), p. 26, tables 18, 44; (1910), p. 147.

*P. lunula,* Lemmermann (1899), p. 358; (1901), p. 358; (1902), p. 260; (1905*a*), p. 20.

*P. lunula,* Murray and Whiting (1899), pp. 337, 339, 340, tables 5–9.

*P. lunula,* Ostenfeld (1899), tables 3, 5, 6; (1900), tables 5, 7; (1906), p. 6; (1909), p. 7; (1913), pp. 339, 344, 476.

*P. lunula,* Schröder (1900), p. 13; (1906), pp. 321, 327, 330, 339; (1911), pp. 620, 626, 651.

*P. lunula,* Ostenfeld and Schmidt (1901), p. 177.
*P. lunula,* Schmidt (1901), p. 138.
*P. lunula,* Blackmann (1902), pp. 183, 187, fig. 8.
*P. lunula,* Entz, Jr. (1902), p. 92; (1905), p. 108; as *Gymnodinium lunula* (1907), p. 22; (1909), p. 261.
*P. lunula,* Lohmann (1902), p. 52; (1908), pp. 168, 325, 326.
*P. lunula,* Ostenfeld and Paulsen (1904), p. 170.
*P. lunula,* Karsten (1905), p. 33; (1906), pp. 188, 201; (1907), pp. 233–532, tabulated references.
*P. lunula,* Pavillard (1905), pp. 46, 101.
*P. lunula,* Apstein (1906), pp. 263–269; (1909), pp. 1–27.
*Gymnodinium lunula,* Dogiel (1906), pp. 1, 2, 4–20, pl. 1, figs. 1–25 (figure 20 is not of the same species as shown in figures 22–25).
*Pyrocystis lunula,* Zacharias (1906), p. 509.
*P. lunula,* Chatton (1907), p. 284.
*P. lunula,* Gough (1907), pp. 190, 192.
*P. lunula,* Okamura (1907), p. 135, pl. 5, fig. 32; (1912), p. 5.
*P. lunula,* Wright (1907), p. 4, pl. 1, figs. 3–5.
*P. lunula,* Paulsen (1908), pp. 110, 111, figs. 153–154.
*Gymnodinium lunula,* Caullery (1910), p. 211.
*Pyrocystis lunula,* Jollos (1910), p. 203.
*P. lunula,* Wille (1910), p. 296.
*P. lunula,* Doflein (1911), p. 524, figs. 467, 468.
*P. lunula,* Mielcke (1911), pp. 328, 338.
*Diplodinium lunula,* Klebs (1912), pp. 389, 390, 442, 443, fig. 4.
*Gymnodinium lunula,* Kofoid and Ridgen (1912), p. 336.
*Pyrocystis lunula,* Schiller (1912), p. 28.
*P. lunula,* Cavers (1913), pp. 182, 184, figs. $9_{27-34}$.
*P. lunula,* Poche (1913), pp. 161, 162.
*Gymnodinium lunula,* Pascher (1916), p. 132.
*Dissodinium lunula,* Pascher (1916), p. 131, fig. 3*a*.
*Pyrocystis lunula,* West (1916), pp. 55, 57, fig. 40.
*P. lunula,* Lebour (1917*b*), p. 198.

DIAGNOSIS.—A small species with ellipsoidal body, its length 1.22 transdiameters: girdle submedian, displaced twice its own width; sulcus extending from apex to antapex; color greenish yellow. Crescentic and spherical *Pyrocystis* stages prevalent. Length, 22μ. Cosmopolitan in neritic marine habitat.

DESCRIPTION.—The body is broadly ellipsoidal, circular in cross-section, tapering slightly or rounded at the apices, its length 1.22 transdiameters at the widest part. The epicone and hypocone are subequal in size. The epicone is rounded conical in outline with convex sides and rather broad apex. It has a length on the left and right sides of about 0.45 and 0.5 respectively of the total length of the body. The hypocone is usually slightly more hemispherical than the epicone, with broader antapex.

The girdle is submedian in position, its proximal and distal ends having a distance from the apex of 0.45 and 0.5 respectively of the total length of the body. The furrow has a width of about 0.14 transdiameter and is deeply impressed with overhanging borders. The sulcus extends in a nearly straight line from the apex to the antapex as a wide, deep furrow. The anterior flagellar pore opens at the proximal junction of girdle and sulcus, the posterior pore a slight distance posterior to the distal one.

The nucleus is a large ellipsoidal body near the center of the organism. Its major and minor axes are about 0.5 and 0.3 transdiameter in length respectively.

The cytoplasm is clear and finely granular. No pusules have been observed. The color is greenish yellow. These small forms have not been positively identified after leaving the cyst, hence nothing can be said in regard to their nutrition and activities. Very many small individuals of this genus have been observed in the material under examination, but the rapidity of their movements has prevented a critical examination.

LIFE CYCLE.—*Gymnodinium lunula* is one of the very few members of this group of which we have any definite knowledge of more than one stage of its life cycle.

Schütt (1895–96) figured the crescent-shaped encysted forms and suggested their connection with *Pyrocystis noctiluca* Murray (1885), but it was not until the publication of Dogiel's (1906) studies on this species that the connection between these and the large globular forms, similar to or identical with *P. noctiluca*, was established.

Owing to a complete lack of knowledge of the development of the dinoflagellates, the discovery of these stages was given a greater importance than facts later revealed warranted. As a result these species were isolated from *Gymnodinium* and placed in a separate family of algae, Pyrocystiae, by Blackman (1902). It has been pointed out elsewhere in this paper that indications lead to the conclusion that these stages are normal ones in the life cycle of many forms, including *Gonyaulax, Gymnodinium,* and *Gyrodinium,* and that the spheroidal or variously shaped, non-motile cysts probably are a part of the developmental cycle of most of the dinoflagellates. Dogiel (1906) pointed out the desirability of further investigation before separating *Gymnodinium lunula* from the rest of the genus, and his conclusions are confirmed by later work.

The life cycle, or the part thus far brought to light, may be divided into three parts, the relative lengths of which are unknown. One of these is the huge globular cyst, largely filled with vacuoles with the nucleus and most of the cytoplasm localized at one side close to the periphery, from which protoplasmic strands extend out to the enclosing wall (fig. I, 1). This cell divides into eight or sixteen moieties within the primary cyst and each of these parts in turn becomes enclosed in slender crescentic secondary cysts (fig. I, 3, 4). This process produces the second part or stage shown in plate 3, figure 55. The contents of these cysts may divide into two or as many as eight moieties, each of which develops a girdle, a sulcus, and the two flagella (fig. I, 7) and breaks out of the cyst as a typical *Gymnodinium*. During the third part of this cycle the individual may divide, either in the motile condition or on encystment (fig. I, 9–11). This may be repeated many times apparently before any further change takes place. What occurs between this stage and the production of the large spherical primary cyst is as yet unknown.

DIMENSIONS.—Length, 22$\mu$; transdiameter, 17$\mu$; axes of nucleus, 7$\mu$ to 10$\mu$ and 5$\mu$ to 7$\mu$; length of crescent-shaped cyst, 104$\mu$; diameter of large globular cyst, 155$\mu$.

OCCURRENCE.—The exact occurrence and distribution of this species is hard to define, since it has been confused in literature with several other similar forms, as may be seen in an examination of Schütt's figures (1895, 1896), as well as those of Dogiel (1906). It is apparently cosmopolitan in the marine habitat, having been recorded as *Pyrocystis* from nearly every sea where dinoflagellates have been studied. It is abundant at La Jolla in the surface plankton during most of the summer.

SYNONYMY.—Claparède and Lachmann (1858–61) early described these cysts from Bergen, Norway, as developmental stages of *Peridinium*. First figured by Schütt (1895) as *Gymnodinium lunula*, he later (1896) changed the name of this species to *Pyrocystis lunula*. Dogiel (1906) recommended its inclusion in the genus *Gymnodinium* as *G. lunula*. Klebs (1912) further added to the confusion already existing by creating for it a new genus, *Diplodinium*, disregarding the fact that that name was already preoccupied by a ciliate in the group Protista, *Diplodinium* Schuberg. Following the usage of Schütt and the suggestion of Dogiel, we regard this species as a valid one in the genus *Gymnodinium*, and base its allocation on the affinities revealed by the motile biflagellate stage, as elsewhere in the Gymnodinioidae. It appears better to await a fuller knowledge of life histories of *Gymnodinium* before accepting Pascher's (1916) allocation of this species in a separate genus as he has done in erecting *Dissodinium* for it.

Its affinities within the genus are obscured by our lack of knowledge of the smaller representatives of this genus. It is close to the species *G. scopulosum* in its subconical form, but is much smaller (22μ) than that species (47μ), and lacks its overhanging epitheca.

Closer inspection of the spheroidal and cresentic cysts referable to this species is needed to determine whether or not they may include phases of several species.

### **Gymnodinium marinum** Saville-Kent

Text figure X, 13

*Gymnodinium marinum* Saville-Kent (1880–82), p. 444, pl. 25, figs. 60–61.
*G. marinum*, Bütschli (1885), p. 1017.
*G. marinum*, Entz, Jr. (1902), p. 125; (1907), p. 17; (1909), p. 253.

DIAGNOSIS.—A minute species with broadly ovoidal body, dorsoventrally compressed, its length 1.03 transdiameters; girdle premedian, without displacement; sulcus extending from girdle to antapex; colorless, holozoic. Length, 30μ. Infusion of hay and sea water from St. Heliers, Jersey, March.

DESCRIPTION.—The body is broadly oval in ventral view with broad apices, widest posteriorly, its length 1.03 transdiameters at the widest part. It is compressed dorsoventrally to about 0.62 of the widest transdiameter, and in lateral view is reniform with convex dorsal and concave ventral surface. The hypocone exceeds the epicone in length and in width. The epicone is hemispherical in ventral view with symmetrically rounded sides. Its length is 0.4 of the total length of the body. The hypocone is hemispherical posteriorly, widest in the central part and tapering anteriorly at the girdle, in ventral view.

The girdle is slightly premedian, its distance from the apex about 0.4 of the total length of the body. It forms a complete circle around the body and is deeply impressed. The sulcus extends from the girdle to the antapex in a straight line. The longitudinal flagellum arises at the proximal end of the sulcus.

The nucleus is not figured by Saville-Kent (1880–82). The cytoplasm is clear and transparent and usually contains numerous spherules varying in size. Nutrition is holozoic. Saville-Kent observed it actively devouring *Heteromita* and other monads in the same culture, the organisms being taken in at the sulcal region near the girdle.

Dimensions.—Length, 30$\mu$; transdiameter, 28$\mu$; dorsoventral diameter, 17$\mu$.

Occurrence.—Figured by Saville-Kent (1880–82) from an infusion of hay and sea water made at St. Heliers, Jersey, in February. One month later the culture was abundantly filled with these small holozoic forms.

Comparisons.—This species finds its nearest relative, apparently, in *G. cinctum*, a species with ochraceous chromatophores. *G. cinctum,* however, does not show the same dorsoventral compression of the body found in this species, and has a smaller epicone.

## **Gymnodinium minor** Lebour

Text figure X, 12

*Gymnodinium minor* Lebour (1917*b*), p. 192, fig. 8.

Diagnosis.—A minute species with stout ovoidal body, its length 1.16 transdiameters; girdle displaced by narrowing its furrow; sulcus extending from the girdle to the antapex. Length, 28$\mu$. Plymouth Sound, England, May–July.

Description.—The body is rotund ovoidal with the widest part anterior, its length 1.16 transdiameters at the widest part. The epicone exceeds the hypocone in length by about 0.5 of its own length. It is subhemispherical in shape with a length on the left and right sides of the sulcus of 0.46 and 0.6 respectively of the total length of the body. The hypocone is slightly narrower than the epicone with truncate antapex.

The girdle is behind the midregion of the body, joining the sulcus about 0.64 of the total length of the body from the apex. On the right side the furrow becomes contracted to less than 0.3 its own width, giving an appearance of displacement contradicted by the posterior borders of the girdle. It is wide on the left side of the body, about 0.06 transdiameters, and deeply impressed. The sulcus extends from the girdle to the antapex, widening as it passes posteriorly.

The nucleus is an ellipsoidal body near the center of the body. Coarse chromatin strands extend obliquely along its major axis. Its major and minor axes are about 0.5 and 0.25 transdiameter in length respectively. Several green food masses were present in the anterior part of the body.

Dimensions.—Length, 28$\mu$; transdiameter, 24$\mu$; axes of nucleus, 12$\mu$ and 6$\mu$.

Occurrence.—It has been figured by Lebour (1917*b*) from Plymouth Sound, England, from collections made from May to July.

Comparisons.—This species is nearest to *G. ovulum* sp. nov. (fig. X, 15), but differs from it in the less spheroidal form (probably distended), greater displacement of the girdle, and lack of sulcus on the epicone.

## **Gymnodinium mirabile** Penard

Text figure X, 18

*Gymnodinium mirabile* Penard (1891), pp. 11, 14, 16, 22, 23, 24, 25, 30, 56, pl. 5, figs. 1–7.
*G. mirabile,* Imhof (1892), p. 175.
*G. mirabile,* Lemmermann (1900), p. 116; (1902), p. 260; (1910), p. 613, figs. 15–16; pp. 618, 624.
*G. mirabile,* Levander (1901), p. 6.
*G. mirabile,* Schilling (1913), p. 16, fig. 14.

DIAGNOSIS.—Medium large species with subovoidal body, dorsoventrally flattened, its length 1.28 transdiameters; girdle displaced about its own width; sulcus short on epicone and extending to antapex; chromatophores green, yellow or brown. Length, 90$\mu$. Lake Geneva, Switzerland.

DESCRIPTION.—The body is stout, subovoidal, with broad apices, widest below the middle, its length 1.28 transdiameters at the widest part. The epicone exceeds the hypocone in length by about 0.18 its own length. It is campanulate with broad apex, and a length on the left and right sides of 0.5 and 0.54 respectively of the total length of the body. The hypocone is slightly broader than the epicone, with a broad antapex which is truncate or notched.

The girdle is slightly behind the median part of the body and is displaced posteriorly about its own width. The furrow is narrow and is deeply impressed with high rounded borders. The sulcus invades the epicone for about half its length and extends posteriorly to the antapex.

The nucleus is a small, ellipsoidal body in the middle of the hypocone filled with coarse, chromatin strands. Its major and minor axes are about 0.35 and 0.28 transdiameter in length respectively. The peripheral zone of cytoplasm is filled with elongated, rodlike chromatophores, radially arranged, and green, yellow, or brownish in color.

DIMENSIONS.—Length, 90$\mu$; transdiameter, 65$\mu$; axes of nucleus, 20$\mu$ and 25$\mu$.

OCCURRENCE.—This species was figured by Penard (1891) from Lake Geneva, Switzerland.

RELATIONSHIPS.—This species is close to *G. uberrimum* (Allman), described by Penard (1891) as *G. mirabile* var. *rufescens*, but differs from it in proportions, being a relatively longer form with greater displacement of the girdle.

## **Gymnodinium monadicum** (Perty) Saville-Kent

Text figure BB, 7

*Peridinium monadicum* Perty (1852), p. 162, pl. 7, fig. 15.
*Gymnodinium monadicum* Saville-Kent (1880–82), pp. 443, 444.

DESCRIPTION.—A minute form with ovoidal to ellipsoidal body, widest anteriorly, with rounded apices. Epicone is much wider than the hypocone with the girdle slightly postmedian. The color is green with a small, red pigment spot. Length, 16$\mu$. Fresh water from the Bernese Alps, Switzerland.

SYNONYMY.—Figured by Perty (1852) as *Peridinium monadicum,* it was placed in the genus *Gymnodinium* by Saville-Kent (1880–82) as *G. monadicum.* He considers this identical with *G. vorticelli* (our fig. X, 29), described by Stein

(1878). Stein's species differs in its proportions and in the lack of a red pigment spot. The ventral face of Perty's form has not been figured, hence that part of the organism cannot be compared with *G. vorticella.* Until further work has established its definite morphological characters, this form must be considered as a doubtful species not identifiable with existing data.

### **Gymnodinium monas** (Ehrenberg)

*Peridinium monas* Ehrenberg (1840), p. 201; (1845), p. 18.
*Heteraulacus ? monas* Diesing (1850), p. 101.
*Heteroaulax ? monas* Diesing (1866), p. 95.
*Peridinium monas,* Claparède and Lachmann (1858–61), p. 406.
*P. monas,* Maggi (1874), p. 118; (1880*a*), pp. 9, 13; (1880*b*), pp. 309, 313.
*P. monas,* Stein (1878), p. 60.
*P. monas,* Saville-Kent (1880–82), p. 444.

Ehrenberg (1840) has described as *Peridinium monas* an organism which Saville-Kent (1880–82) considered as possibly identical with *Gymnodinium marinum.* Ehrenberg's description, without figures, hardly furnishes an adequate basis for the systematic allocation of this small form. He has described it as very small, obtuse, without horns, and remarkably social, its diameter 43µ and occurring in the Baltic Sea. The absence of a theca would remove it from the genus *Peridinium,* but the lack of further data leave it permanently indeterminable.

### **Gymnodinium multilineatum** sp. nov.

Plate 5, figure 59; text figure Y, 18

Diagnosis.—A rather large species, with symmetrical, broadly fusiform body, apex rounded, antapex more contracted, bullet-shaped, its length about 2 transdiameters, both with minute points; girdle slightly displaced; surface with fine striae, about 50 on one face; colorless; nucleus central. Length, 108µ. Pacific off La Jolla, California, July, August.

Description.—The body is broadly fusiform, perfectly symmetrical, circular in cross-section, its length 2.25 transdiameters. The epicone is about 1.66 of the length of the hypocone, and 0.9 transdiameter in length, rotund ellipsoidal, apex broadly rounded, with a minute apical point. The hypocone is 1.35 transdiameters in length, shaped like the nose of a bullet, the antapex contracting symmetrically to a sharp point.

The girdle is 0.4 of the total length of the body from the apex, almost in transverse plane, both proximally and distally the ends deflected for less than their width posteriorly. The distal end in one individual was displaced posteriorly about its own width with almost no overhang of the proximal end over the distal one. The transverse furrow is deeply impressed, and excavated below the sharp-edged lips. The flagellar pore of the transverse flagellum is an elliptical opening just posterior to the proximal end of the furrow on the left side of the longitudinal furrow. The transverse flagellum is a thin, narrow ribbon almost completely encircling the

body. The sulcus extends anteriorly on the epicone for 0.85 of its length, and posteriorly on the hypocone for little more than 0.33 of its length, fading out at the pore of the longitudinal flagellum at its posterior end. It is linear, lies in the median plane, and forms a narrow, uniform channel about half the width of the transverse furrow, flaring slightly only in the anterior part.

The surface is characteristically marked with very fine, delicate, close-set longitudinal striae of uniform intervals on both epicone and hypocone. These anastomose or die out distally so that the uniformity of interval is maintained throughout the whole surface. At the girdle there are about fifty of these striae on one face of the body. Beneath the pellicle there is a thin layer of faintly developed slender rodlets about 0.06 transdiameter in length. These stand perpendicularly to the surface except in the antapex, where they are somewhat larger and are crowded into the narrowing apex. Scattered spheroidal refractive granules lie just beneath this layer of rodlets.

The body as a whole is quite translucent and of a greyish color tinged faintly with greenish yellow. It is crowded with numerous spherical pinkish vacuoles 0.06 to 0.12 transdiameter in diameter. The broadly ellipsoidal nucleus lies just beneath the girdle with its long axis inclined to the right anteriorly. It is about 0.5 transdiameter in length in its greatest axis, and is filled with a coarse, moniliform chromatin thread. No chromatophores and no pusules could be detected. A few small refractive granules were clustered near the nucleus. Probably holozoic.

Dimensions.—Length, 108μ; transdiameter, 50μ; greatest diameter of nucleus, 26μ.

Occurrence.—This was taken July 5, 1917, with a No. 12 silk net, in a haul 6 miles off La Jolla, California, from 80 meters to the surface and in a surface temperature of 21.4 C. On July 11 it was taken with a No. 25 silk net, 4 miles off La Jolla, in a haul from 80 meters to the surface, and on July 27 and on August 21 at the same place and under approximately the same conditions.

Comparisons.—The structure of the girdle places this species in the genus *Gymnodinium*, but the striate surface and rodlets recall those of many species of *Gyrodinium*, such as *G. acutum*. It belongs to the subgenus *Lineadinium*, but has no near relatives in form, proportions, or size. It is the most finely striated species in the genus and appears to be a unique and isolated type.

### **Gymnodinium multistriatum** sp. nov.

Plate 4, figure 37; text figure Y, 1

Diagnosis.—A medium sized species with biconical body, its length 1.47 transdiameters; girdle submedian, displaced 0.25 transdiameter; sulcus extending from apex to antapex; surface finely striate; color grey green and yellow ochre. Length, 100μ. Pacific off La Jolla, California, August.

Description.—The body is rotund biconical, asymmetrical, almost rhomboidal in shape, nearly circular in cross-section, with rounded apices, its length 1.47 transdiameters at the widest part, which is equatorial. The epicone is slightly larger than the hypocone in size, its length being greater by 0.1. It has the form of a cone of about 65°, with a blunt apex and broad base, its right side about 0.23 longer than its left side. The right side is slightly more convex than the left. It has a length on the left and right sides of 0.43 and 0.59 respectively of the total length of the body. The hypocone forms a cone of about 70° with its left side longer than the right and a blunt antapex excavated on the ventral side by the sulcal notch. Both sides are only very slightly convex.

The girdle is submedian, its proximal and distal ends having a distance from the apex of 0.43 and 0.59 respectively of the total length of the body. It makes a slight anterior deflection in the first 0.12 of its course, beyond which it takes a descending left spiral course around the body, displaced posteriorly at its distal end 0.25 transdiameter. The furrow is wide, about 0.07 transdiameter, and relatively shallow, with smooth borders. The sulcus extends from the apex to the antapex in a nearly straight line. The furrow is slightly narrower than the girdle and lies in a wide trough (about 0.5 of the transdiameter in the middle of the body) which extends down the ventral face of the organism, deepest in the girdle region and posteriorly, fading out near the apex. Beyond the posterior pore the sides are deflected laterally, forming a wide excavation at the antapex. The anterior flagellar pore opens near the lower border of the girdle at its proximal junction with the sulcus, the posterior pore a short distance anterior to the antapex.

The nucleus is spherical and is located just below the equatorial plane on the left side of the body. Its chromatin contents could not be analyzed. Its axis is 0.35 transdiameter in length.

The cytoplasm is finely granular and densely filled with large vacuoles, pinkish grey in color. In the peripheral zone are numerous blue-green oil droplets and dark, refractive granules, evidences of holozoic nutrition. A small sacklike pusule opens into each flagellar pore. The surface is striate with closely placed, equidistant, blue-green striae. The number of striae on the hypocone exceeds the number on the epicone by about 0.25. The color of the cytoplasm is pearl grey with minute stippling of yellow ochre at the apices and near the girdle.

Dimensions.—Length, 100$\mu$; transdiameter, 68°; transdiameter of nucleus, 24$\mu$.

Occurrence.—A single individual was taken August 21, 1917, with a No. 25 net, 5 miles off La Jolla, California, in a haul from 83 meters to the surface.

Comparisons.—In the fineness and number of surface striae this species closely resembles *G. multilineatum* sp. nov. (fig. Y, 18), *G. radiatum* sp. nov. (fig. Z, 9), and *G. rubrum* sp. nov. (fig. Y, 4) in the relatively wide displacement of the girdle. In the latter respect these two species approach the *Gyrodinium* type of girdle. It belongs in the subgenus *Lineadinium* in a group of subbiconical to broadly ellipsoidal, rather finely striate species, including *G. situla, G. diploconus,* and *G. radiatum,* and has the maximum degree of displacement of the girdle in this group.

## **Gymnodinium musei** Danysz

Text figure X, 3

*Gymnodinium musei* Danysz (1887), pp. 238, 239.
*G. musaci,* Pouchet (1887), pp. 89, 104, pl. 10, fig. 6.
*G. musci,* Entz, Jr. (1909), pp. 262, 268. *Lapsus.*
*G. musei,* Lemmermann (1910), p. 565, figs. 13–15, pp. 618, 619, 622.

Diagnosis.—A minute species with broad body, its length 1.22 transdiameters; girdle posterior, without displacement; sulcus on hypocone only; two minute red pigment spots. Length, 20$\mu$. Fresh-water pools, Paris, France.

Description.—The body is broadly ellipsoidal in ventral view with broad apices, dorso-ventrally compressed, its length 1.22 transdiameters at the widest part. The epicone greatly exceeds the hypocone in size, its length being greater by 0.53. It is elongate hemispherical in

shape, flaring posteriorly, with a length of 0.69 of the total length of the body. The hypocone is rounded truncate, slightly notched by the distal end of the sulcus.

The girdle is posteriorly placed, its distance from the apex being 0.69 of the total length of the body. It forms a complete circle around the body, the ends meeting without displacement. The furrow deeply undercuts the anterior border of the epicone and is almost obscured by the lip thus formed. The sulcus extends from the girdle to the antapex. The flagella were not figured by Pouchet (1887), whose figures form the basis of this description.

The interior of the body is filled with numerous spherules, among which the nucleus is not distinguished. Two minute red pigment spots are found ventrad posterior to the junction of the girdle and sulcus. Pouchet (1887) figures four schizonts within an ellipsoidal cyst approximately the size of the free flagellate. In his figure 6 D, plate 10, Pouchet has figured a form which evidently does not belong to the species, *G. musei*, differing too greatly in proportions from his figures 6 A and 6 B to have any close relationship with them.

Dimensions.—This was described but not figured by Danysz (1887) from pools at Paris, France. In the same year Pouchet figured this form in material taken from the same place.

Synonymy.—Entz (1909) quotes Danysz's description of this species with the species name spelled *musci*, a *lapsus* for *musei*.

Comparisons.—The description and figures of this species are so inadequate that comparisons are tentative. It appears to be unique in the excessively large epicone, which has nearly three times the volume of the hypocone. The nearest approach to these proportions appears in *G. vorticella* Stein (fig. X, 29) and *G. dissimile* sp. nov. (fig. X, 32). The stigma in all of Pouchet's figures (1887) is double, consisting of a larger and smaller parallel moiety, a condition of this organ unique in this genus.

### **Gymnodinium ovulum** sp. nov.

Plate 5, figure 58; text figure X, 15

Diagnosis.—This is a minute species with spheroidal body, its length and transdiameter subequal; girdle submedian, without displacement, sulcus short on both epicone and hypocone; colorless. Length, 28μ. Pacific off La Jolla, California, July, August.

Description.—The body is spheroidal, circular in cross-section, apices broad and rounded, its length and transdiameter equal. The hypocone is very slightly larger than the epicone. The epicone is subhemispherical in shape, its sides less convex than those of the hypocone. The apex is broad and smoothly rounded. It has a length of 0.44 of the total length of the body. The hypocone is hemispherical in shape with smoothly rounded sides and broad antapex.

The girdle is submedian in position, its distance from the apex 0.44 and from the antapex 0.46 of the total length of the body. The furrow is wide, about 0.1 transdiameter, and deeply impressed, its sides gradually curving outward to the surface of the body. The sulcus is a shallow trough beginning midway between girdle and apex and extending to within a short distance of the antapex. It follows a slightly sinuous course, enlarging at the girdle, narrowing toward both ends. The anterior flagellar pore opens at the junction of the girdle and sulcus, the posterior pore a short distance below.

The nucleus is a relatively large, ellipsoidal body filled with coarse, moniliform chromatin strands. It is located on the left side of the anterior part of the body. Its major and minor axes are 0.53 and 0.42 transdiameters respectively.

No pusules were observed. The cytoplasm is finely granular and usually contains one or more large food bodies. The one figured contained a single large, reddish brown mass, nearly filling the entire body. Other individuals showed one to several food bodies yellow ochre in color. Nutrition is holozoic. The color of the cytoplasm is pearl grey. It is made conspicuous under the microscope by the presence of the brightly colored food bodies.

Dimensions.—Length, 28μ; transdiameter, 28μ; axes of nucleus, 15μ and 12μ.

Occurrence.—This was observed July 9, 1914, in a surface haul taken near the shore at La Jolla, California. In July and August, 1917, it was frequently met with in most of the hauls made. The one figured was taken July 21, with a No. 25 net in a surface haul at the end of the pier.

Comparisons.—The group of minute species represented by *G. ovulum*, *G. minor*, *G. vorticella*, *G. marinum*, and a few fresh-water forms must be regarded only tentatively as good species. The similarity of these forms to the small *Gymnodinium* found in cysts, evidently the products of multiple fission, leads one to suspect that we may be dealing here with a stage in the life history and not with distinct species. The great difficulty in following the development of these extremely delicate organisms leaves this an open question at the present time. For the sake of convenience, therefore, they are held as valid species until their development has been followed out more fully. Among marine species *G. ovulum* is nearest *G. minor* Lebour (fig. X, 12) and *G. flavum* sp. nov. (fig. X, 7), but is more nearly spherical than either and lacks the chromatophores of the latter. The distension of the body by the food balls is possibly a factor in its spheroidal contour.

### **Gymnodinium pachydermatum** sp. nov.

Plate 3, figure 32; text figure AA, 5

Diagnosis.—This is a large species of robust habit, body broadly ellipsoidal, its length 1.53 transdiameters; epicone hemispherical; girdle submedian; displaced twice its own width; sulcus invading the epicone, extending to the antapex; differentiated ectoplasm; color orange green. Length, 160μ. Pacific off La Jolla, California, June, July.

Description.—The body is of robust habit, broadly ellipsoidal with broad apices, nearly circular in cross-section, with protuberant girdle, its length 1.53 transdiameters at the widest part. The epicone and hypocone are subequal in length, but the transdiameter of the distal part of the epicone is slightly greater than the greatest transdiameter of the hypocone. The epicone is broadly dome-shaped, hemispherical anteriorly and flaring slightly at the girdle. The apex is broad and symmetrically rounded. The epicone has a length on the left and right sides of 0.4 and 0.53 respectively of the total length of the body. The hypocone is somewhat narrower than the epicone with sides subparallel anteriorly and rounded posteriorly with the antapex deeply notched by the distal end of the sulcus.

The girdle is submedian, its proximal end meeting the sulcus at a distance from the apex of 0.4 of the total length of the body. It sweeps around the body in a descending left spiral direction, displacing the distal end about twice the width of the girdle. The furrow is wide, about 0.05 transdiameter, and is deeply impressed with overhanging shelflike borders, its upper lip cut under and the lower one gradually rounded. The sulcus begins midway between the girdle and apex and extends posteriorly to the antapex as a deep trough. In the antapical region the borders are widely deflected and the trough deepened, forming a deep excavation notching the antapex. The anterior flagellar pore opens at the junction of the proximal end of the girdle and sulcus, the posterior pore a short distance below the distal junction.

The nucleus is a large spherical body in the central part of the hypocone near the left of the sulcus in ventral view. Its axis is about 0.32 transdiameter.

No pusules were observed in the individual figured. The cytoplasm is granular and generally contains many cell inclusions. In the epicone was an irregularly shaped food mass, pale lumière green in color near which was a group of 6 very large spherical bodies of varying shades of cream color and yellowish green. Around these were smaller vacuoles filled with the pink fluid usually present in the pusules, a number of which were also scattered through the hypocone. Behind the distal junction of the girdle and sulcus was a rounded body, dark green in color. Radiating out from this was a group, 10 in number, of long, slender, tapering green rodlets. These varied in length from $22\mu$ to $40\mu$. The differentiated ectoplasm was remarkably clear and striking even under the lowest power of the microscope, where it had the appearance of a wide, clear band surrounding the organism. A closer examination showed it to be composed of two layers, a hyaline double-contoured layer superimposed upon which was a somewhat narrower one of alveoli, the rounded outer surfaces of which gave a ridged, uneven appearance to the outline of the body. The inner layer, like that in *G. dogieli,* was yellow, the alveolar orange in color on the hypocone shading to lighter tones of the same on the epicone. The whole color effect was rich and striking.

Dimensions.—Length, $160\mu$; transdiameter, $104\mu$; axis of nucleus, $34\mu$.

Occurrence.—This was taken June 27, 1917, with a No. 12 silk net, in a haul 6.1 miles off La Jolla, California, from 120 meters to the surface and in a surface temperature of 20° C. Another individual was observed on July 11 with a No. 25 silk net, in a haul 4 miles off La Jolla, from 80 meters to the surface and in a surface temperature of 20° C. On July 20 a third individual was taken 6 miles off La Jolla with the same apparatus and at the same depth, in a surface temperature of 20°5 C.

Comparisons.—This, with *G. dogieli* sp. nov., *G. amphora* sp. nov., and *G. abbreviatum* sp. nov. (figs. AA, 8, 6; fig. Z, 7), form the most striking representatives of the subgenus *Pachydinium*. They are closely related with the same differentiation of ectoplasm and endoplasm and are remarkably beautiful in coloring, the reproductions of which fail to do them justice. They are the most highly organized of the genus, and form the culmination of a line of development which may be traced from the simpler forms. This species has a posterior sulcal notch not present in the others named, and a greater displacement of the girdle.

## **Gymnodinium palustre** Schilling

Text figure X, 16

*Gymnodinium palustre* Schilling (1891), pp. 248, 277, 278, pl. 9, figs. 11–13, pl. 10, fig. 11; (1913), p. 16, fig. 11.

*G. palustre*, Ludwig (1898), p. 299.

*G. palustre*, Mez (1898), p. 216, pl. 6, fig. 285. Based on Schilling's (1891) figures.

*G. palustre*, Lemmermann (1889), p. 126; (1900), p. 116; (1901), pp. 67, 69, 72; (1902), p. 260; (1905), p. 159; (1910), pp. 613, 618, 620, figs. 15, 16.

*G. palustre*, Schönichen and Kalberlah (1910), p. 232; (1909), p. 252. Based on Schilling's (1891) figures.

*G. palustre*, Bolochonzew (1903), pp. 7, 59.

*G. palustre*, Wesenberg-Lund (1904), pp. 106, 107 (in part = *G. zachariasi*).

*G. palustre*, Entz (1910), p. 158.

*G. palustre*, Guyer (1910), pp. 365, 377.

*G. palustre*, Kolowitz (1911), pp. 314, 315, 325, 326, 327, 341, 357, pl. 6, fig. 2 (in part = *G. zachariasi*), pl. 10, fig. 4; (1912), p. 214.

Not *Gymnodinium palustre*, Zacharias (1899); Dogiel (1906); Klebs (1912); nor Fauré-Fremiet (1914) (= *G. zachariasi* (Zach.) Lemm.).

Diagnosis.—A small species with ellipsoidal body, its length 1.12 transdiameters; girdle without displacement; yellow to brown chromatophores. Length, 44$\mu$. Fresh-water ponds and swamps in Germany and Switzerland in summer.

Description.—Body stout ellipsoidal, the anterior end rounded, the posterior truncate, its length 1.12 transdiameters at the widest part. The epicone exceeds the hypocone in length by 0.4 its own length. It is bell-shaped with rounded apex. The hypocone is broadly rounded with the antapex more or less truncate.

The girdle is postmedian in position, its length from the apex about 0.4 of the total length of the body. The furrow is deeply impressed, with overhanging borders. A sulcus is not figured by Schilling (1891). The nucleus is located in the central part of the body. Round, yellow to dark brown chromatophores are scattered through the peripheral zone of cytoplasm.

Dimensions.—Length, 44$\mu$; transdiameter, 37.5$\mu$. As figured by Schilling (1891, pl. 10, fig. 11; 1913, fig. 11) the transdiameter is 15$\mu$, though not so given in the text.

Occurrence.—This species was found by Schilling (1891) in ponds and ditches in Germany. Guyer (1910) notes its abundance in the summer plankton in the Greifen Lake in Switzerland. Lemmermann (1902) records it from Lake Plön, and (1905) from Oppeln, Germany. Bolochonzew (1903) found it occurring in the summer in the Volga River, Russia, and Kolkwitz (1911) in Taken, Russia, and Remscheid, Germany, throughout the year.

Comparisons.—This species is near *G. zachariasi* in its proportions, but is somewhat stouter. The chromatophores also appear to differ, being rodlike in the latter and more rounded in *G. zachariasi*. No pseudopodia have been noted in this species.

### **Gymnodinium paradoxum** Schilling

Text figure X, 26

*Gymnodinium paradoxum* Schilling (1891*a*), pp. 278, 279, pl. 10, fig. 13; (1913), p. 18, fig. 15.
*G. paradoxum,* Ludwig (1898), p. 299.
*G. paradoxum,* Mez (1898), p. 216.
*G. paradoxum,* Schönichen and Kalberlah (1900), p. 231; (1909), p. 252.
*G. paradoxum,* Lemmermann (1900), p. 116; (1902), p. 260; (1903*a*), pp. 86, 88, 90, 108; (1905*b*), p. 159; (1908), pp. 170, 180; (1910), pp. 565, 618, 620, 626, fig. 22.
*G. paradoxum,* West and West (1906), pp. 91, 92; (1909*a*), p. 187.
*G. paradoxum,* Klebs (1912), p. 384.
*G. paradoxum,* West (1916), p. 51.

Diagnosis.—A minute species with a broadly ellipsoidal body, its length 1.12 transdiameters; girdle slightly postmedian, without displacement; sulcus very short; dark brown chromatophores. Length, 40$\mu$. Fresh water, Scottish and English lakes, German lakes, February to April, near Basel, Switzerland.

Description.—The body is rotund ellipsoidal, with broad apices, widest in the middle, its length 1.12 transdiameters at the widest part. The epicone exceeds the hypocone in size, its length being greater by 0.27. It is elongated hemispherical in shape, with broad apex. Its length is about 0.57 of the total length of the body. The hypocone is subhemispherical in shape with smoothly rounded antapex.

The girdle forms a complete circle around the body slightly posterior to the midplane. It is rather broad and comparatively shallow. Distinct outlines for the girdle and sulcus are not given in Schilling's figure (1891*a*). The transverse and longitudinal flagella arise near together at the junction of the girdle and sulcus.

The nucleus is not figured by Schilling. The central part of the cytoplasm is filled with dark brown chromatophores. On the ventral side, immediately below the ends of the girdle, is a relatively large, ellipsoidal pigment spot, the color of which is not indicated, though presumably of a red color.

Dimensions.—Length, 40$\mu$; transdiameter, 34.5$\mu$.

Occurrence.—It was figured by Schilling (1891*a*) from fresh-water swamps and ponds near Basel, Switzerland. It is frequently found among vegetation and in the plankton. Other records of its occurrence are as follows: West and West (1909) from the Scottish and English lakes and Lemmermann (1903*a*, 1905*b*), in ponds in Germany, from February to April.

Synonymy.—West and West (1906) mention a variety of this species, *G. paradoxum* var. *major,* from Lough Currane, County Kerry, Ireland, named by Lemmermann. The only data given are its length, 66–75$\mu$, and transdiameter of 61–67$\mu$. It is not figured. Its position and relationship thus cannot be determined, since the proportions of length and transdiameter differ from those of *G. paradoxum.*

Comparisons.—This species is closely related to *G. rotundatum* and *G. viride* in the subgenus *Gymnodinium,* but it is larger and more rotund than these species, differing also from the former in the presence of the eyespot. In size and shape it is near *G. uberrimum,* but the large eyespot and indistinctness of the chromatophores serve to separate it from that species.

## **Gymnodinium pseudonoctiluca** Pouchet

Text figure X, 35

*Gymnodinium pseudonoctiluca* Pouchet (1885*a*), pp. 71–75, 76, 82, pl. 10, figs. 34–37; (1892*a*), p. 87; (1892*b*), pp. 143–150, pl. 11, figs. 1–14; (1894), p. 169.
*G. pseudonoctiluca,* Bütschli (1879), pp. 1078, 1082.
*G. pseudonoctiluca,* Lemmermann (1899), p. 359; (1910), p. 619.
*G. pseudonoctiluca,* Ostenfeld (1903), p. 561.
*G. pseudonoctiluca,* Mingazzini (1904), pp. 98, 99.
*G. pseudonoctiluca,* Paulsen (1908), pp. 97, 99, fig. 135. After Pouchet (1892*b*).
*G. pseudonoctiluca,* Jörgensen (1912), p. 10.
*G. pseudonoctiluca,* Fauré-Fremiet (1914), pp. 41, 43, 44, 45, fig. 11. After Pouchet (1892*b*).
Not *Gymnodinium pseudonoctiluca,* Lebour (1917*b*), p. 188, fig 3 (= *G. fulgens* nom. sp. nov.).

Diagnosis.—A large species with long, subcylindrical body, its length 2.5 transdiameters; girdle anteriorly located, turning posteriorly on ventral side; sulcus extending from girdle to antapex; color greenish. Length, 116μ. Atlantic, Arctic.

Description.—The body is long, subcylindrical, the anterior end conical, the posterior rounded, its length 2.5 transdiameters. The epicone is greatly exceeded by the hypocone in extent, having an average length of less than 0.3 the length of the hypocone. The length of the epicone on the dorsal side is 0.18 of the total length of the body. It extends posteriorly on the ventral side in a slender point with a length of about 0.55 the total length of the body. It is subconical anteriorly (about 55°), flaring widely at the base. According to Pouchet (1892*b*), the entire epicone is retractile and may almost completely disappear within the body. The hypocone is long cylindrical or enlarged posteriorly. Its length on the dorsal side is about 0.78 of the total length of the body.

The girdle is placed far anteriorly, its distance from the apex on the dorsal side being 0.18 of the total length of the body. Both ends turn posteriorly, meeting at a point slightly posterior to the equator. The furrow is narrow, relatively shallow, with overhanging borders. The sulcus is not well defined in any of Pouchet's (1885*a*, 1892*b*) figures. It apparently extends from the girdle to the antapex.

The nucleus is large and spheroidal, and is found near the center of the body. It is nearly surrounded by a granular mass dark greenish brown in color, giving a dense appearance to the central portion of the body. The remainder of the cytoplasm forms radiating strands extending out from the central mass to the periphery, separated by vacuoles. Scattered through the peripheral layer are granules green and brown like those surrounding the nucleus. Anteriorly the cytoplasm has a yellow or orange color.

The most striking and at the same time puzzling feature of this organism is the seemingly temporary or evanescent protrusion which resembles a tentacle. It is rather difficult to harmonize the various figures of this species given by Pouchet (1885*a*, 1892*b*) and his own description does not clear up the difficulties. The girdle in figures 2 and 4, plate 11 (1892*b*), with its posterior turn on the dorsal side, has no apparent relation to the same structure in figures 3 and 7 on the same plate, in which the girdle passes across the dorsal side in a direction at right angles to the long axis of the body. Variations to this extent in one species in the position of the girdle are not known elsewhere in the Dinoflagellata. The tentacle itself apparently arises from the sulcal region near the posterior end of the body as a long, slender, protoplasmic extension

which is not motile, as is the flagellum. Its length is about equal to the dorsoventral diameter or less. It is possible that he is here confusing two distinct forms or that we have in this species an extraordinary mobility in the form of the body.

DIMENSIONS.—Length, 100–200$\mu$; transdiameter, 46–80$\mu$.

OCCURRENCE.—This species was figured by Pouchet (1885*a*) from the Atlantic off Concarneau, France, in June, and, at later dates (1892*b*), from the Atlantic off the Faroe Islands in August, and, in 1894, from the Arctic Ocean near Spitzbergen in August.

SYNONYMY.—Lebour (1917*b*) has figured a form which she calls *Gymnodinium pseudonoctiluca* Pouchet. The differences between the two forms are too great, however, to place it with Pouchet's species. The girdle forms a complete circle at the anterior end, instead of turning posteriorly on the ventral surface, where, in *G. pseudonoctiluca*, it reaches posteriorly beyond the middle region of the body. Lebour's species also possesses bright yellow chromatophores. It is therefore given species rank, with the name *G. fulgens* nom. sp. nov. Pouchet's record (1894) of this species from the Arctic Ocean at a temperature of 2°–3° C may be looked upon with suspicion. It seems improbable that the Gulf Stream could carry, without change, organisms as frail and delicate as these from the warm semitropical waters to the cold Arctic Ocean.

COMPARISONS.—In its cytoplasmic structure *G. pseudonoctiluca* recalls the conditions found in *G. pachydermatum, G. dogieli,* and *G. amphora* (figs. AA, 5, 1, 6). It differs greatly, however, from that group in its lack of a differentiated ectoplasm. In the possession of this tentacle-like protrusion this species might seem to be a connecting link between this group and the Noctilucidae. However, in so far as our knowledge goes, it appears that we are here dealing with a protoplasmic extension of the edge of the sulcus of a temporary nature, perhaps like that figured by Schütt (1895) for *G. rete*, and by Zacharias (1899) for *G. zachariasi*. It is a tentacular pseudopodium, and not a flagellum transformed into a tentacle, and is therefore not homologous with the tentacle of *Noctiluca*.

## **Gymnodinium punctatum** Pouchet

Text figure BB, 18

*Gymnodinium punctatum* Pouchet (1887), pp. 105–107, pl. 10, fig. 7.
*G. punctatum,* Lemmermann (1899), p. 359.
*G. punctatum,* Paulsen (1908), p. 108.

DESCRIPTION.—This is a minute form with broadly ellipsoidal body in ventral view, compressed dorsoventrally to 0.54 transdiameter, its length 1.33 transdiameters. The girdle is median in position, dividing the body into subequal parts. The epicone is hemispherical, the hypocone slightly notched at the antapex. The nucleus is a large, chromatin-filled body in the epicone. A minute red-pigment spot is present near the posterior part of the body. The sulcus and course of the girdle were not figured by Pouchet (1887). Length, 10$\mu$. Atlantic off Concarneau, France.

Pouchet's description of this form leaves the important species characteristics, the relation of girdle and sulcus, undetermined. Paulsen (1908) suggests the possibility of this being a swarm spore. It differs sufficiently from the other forms described to be regarded only tentatively as a valid species. Its exceptionally small size requires verification.

## **Gymnodinium puniceum** sp. nov.

Plate 5, figure 51; text figure Z, 5

DIAGNOSIS.—This is a large species with subovoidal body, its length 1.57 transdiameters; girdle premedian, without displacement; sulcus extending from near apex to antapex; surface sparsely furrowed; color, onion-skin pink. Length, 110$\mu$. Pacific off La Jolla, California, August.

DESCRIPTION.—The body is subovoidal in shape, with broad apices, widest posteriorly, its length 1.57 transdiameters at the widest part. The hypocone greatly exceeds the epicone in size. The epicone forms a slightly irregular dome with broad rounded apex. The left side is more convex than the right, both are slightly irregular. Its length is about 0.32 of the total length of the body. The hypocone is barrel-shaped, with broad antapex. Its greatest transdiameter at about its middle equals its length. The right side is convex, the left concavo-convex anteriorly and convex posteriorly. The sulcal notch is deflected to the right, throwing the two lobes formed by its borders on the dorsal side of the body, to the right of the midplane of the body in ventral view.

The girdle is premedian in position, its distance from the apex about 0.32 of the total length of the body. It forms a complete circle around the body. The furrow is wide, about 0.07 transdiameter, and is deeply impressed, with its anterior lip deeply undercut and its posterior border gradually rounded. Its borders are irregular, following the curves of the surface. The right end of the girdle is somewhat wider than the left. The sulcus begins near the apex and extends posteriorly in a slightly sinuous line to the antapex. It forms a broad channel which fades out near the apex, widens at the girdle and deepens posteriorly, with the overhanging borders narrowing its apparent width near the posterior pore. Near the antapical region the borders become widely deflected and extend around to the dorsal surface of the body, about the deeply excavated antapex. The anterior flagellar pore is found at the junction of the girdle and sulcus, the posterior pore about 0.6 of the distance between that junction and the antapex.

The nucleus is ellipsoidal, its long axis parallel with the long axis of the body. It is situated on the left side of the body, posterior to the girdle. Its major and minor axes are 0.51 and 0.32 transdiameter respectively.

A small sacklike pusule opens into the anterior flagellar pore. None could be detected at the posterior pore. The cytoplasm is finely granular and is almost completely filled with variously colored food bodies. The central part is occupied by a single large mass of a dark color. Surrounding this were smaller bodies and vacuoles of varying shades of grey, yellow ochre and green, with a few small refractive spherules. Nutrition is holozoic. The general color of the organism is onion-skin pink diffused through the cytoplasm, with a slight deepening of the color anteriorly and in the central part of hypocone.

The surface of the body is marked by deep furrows, about 6 across the ventral face. The surface between the furrows is raised into high, rolling ridges. The furrows disappear before reaching the apices and girdle, but the ridges continue to the girdle and antapex, giving to the borders of both a lobed appearance.

Dimensions.—Length, 110μ; transdiameter, 70μ; axes of nucleus, 36μ and 23μ.

Occurrence.—This species is represented by one individual taken August 6, 1917, with a No. 25 silk net 4 miles off La Jolla, California, in a haul from 60 meters to the surface and in a surface temperature of 21°2 C.

Comparisons.—This species is unique in its coloring in the genus *Gymnodinium*. In its surface structure it recalls the conditions found in *A. galbanum*, the surface being more irregular, however, with its high, rolling ridges, than the latter species. *Amphidinium cucurbita* and *Erythropsis scarlatina* also show the same tendency. It belongs in the subgenus *Pachydinium*, and represents the extreme form of sparse striation, with no near relations. The nearest related species are *Gymnodinium coeruleum* and *G. wilczeki* Pouchet (fig. Z, 4, 8), but color and proportions clearly separate these from *G. puniceum*.

## **Gymnodinium pyrocystis** Jörgensen

*Gymnodinium pyrocystis* Jörgensen (1912), p. 10.

Diagnosis.—A large species, stout, its length 1.6 transdiameters; girdle placed far anteriorly with the ends on the ventral side bent posteriorly; colorless. Length, 200μ. North Sea, September, November.

Description.—The body is large, stout, its length about 1.6 transdiameters. The epicone is small, about 0.2 of the length of the hypocone on the dorsal side. It is subconical with apex blunt or truncate. The hypocone is large and broadly rounded, often broader and thicker at the posterior end, truncate or notched with broadly round lobes.

The girdle lies far anteriorly on the dorsal side, both ends curving posteriorly on the ventral side. The sulcus extends from the region of the girdle to the antapex or passes around towards the dorsal side. The nucleus is nearly spherical and is centrally located. The cytoplasm contains an irregular central mass from which strands pass outward to the periphery where they join. It is filled with numerous spherules of varying size, the largest of which are found in the region of the girdle and at the apices.

Dimensions.—Length, 50–200μ; transdiameter, 30–150μ.

Occurrence.—This species has been described without a figure by Jörgensen (1912) from the North Sea in September and November. He also records it as moderately abundant along the west coast of Norway in autumn.

Comparisons.—This species appears to lie near *G. fulgens* (fig. X, 30) and not far from the larger forms of *Amphidinium* such as *A. vasculum*.

## **Gymnodinium radiatum** sp. nov.

Text figure Z, 9

Diagnosis.—A medium sized species with broadly ellipsoidal body in ventral view, slightly flattened dorsoventrally, its length 1.26 transdiameters; girdle slightly premedian, displaced about twice its own width; sulcus short on epicone, extending to near antapex on hypocone; surface very finely striate. Length, 86μ. Pacific off La Jolla, California, June.

DESCRIPTION.—The body is rotund, broadly elliptical in ventral view, dorsoventrally compressed, with broad, rounded apices, its length 1.26 transdiameters at the widest part, its dorsoventral diameter about 0.88 transdiameter. The hypocone is slightly larger than the epicone, its length being greater by 0.15. The epicone is hemispherical in ventral view with symmetrically rounded sides. It has a length on the left and right sides of 0.33 and 0.48 respectively of the total length of the body. The hypocone also has the form of a slightly elongated hemisphere in ventral view with smoothly rounded sides subparallel anteriorly.

The girdle is slightly premedian in position, its proximal end joining the sulcus at a distance from the apex of 0.33 and its distal end 0.48 respectively of the total length of the body. It follows a descending left spiral course around the body, its distal end displaced posteriorly about two widths of the girdle. The furrow is wide, about 0.08 transdiameter, and is shallow with smooth borders. The sulcus invades the epicone but a short distance. It extends posteriorly on the hypocone in a straight line to near the antapex. The trough is wide and about 0.14 of the dorsoventral diameter in depth. The anterior flagellar pore opens at the proximal junction of the girdle and sulcus, the posterior pore at about 0.3 of the distance between the distal junction and the antapex.

The nucleus is a spheroidal body, found in the center of the organism. Its axis is about 0.43 transdiameter in length. The cytoplasm is granular and is arranged in radial strands, surrounding oblong vacuoles which extend from near the nucleus to the periphery. In surface view these vacuoles give the organism a coarsely vacuolate appearance, with alveoli varying in size. The surface is striate, with fine, longitudinal lines, placed closely together and equal in number on both epicone and hypocone, and about fifty across the ventral face.

DIMENSIONS.—Length, 86μ; transdiameter, 19μ; dorsoventral diameter, 59μ; axis of nucleus, 27μ.

OCCURRENCE.—A single individual was taken June 23, 1904, 13 miles off La Jolla, California, with a No. 20 silk net, in a haul from 265 meters to the surface.

COMPARISONS.—This is the most symmetrically rotund species in the subgenus *Pachydinium*. It lacks entirely the mammillated surface and any outer alveolar layer, characteristic of that subgenus and, in consequence, might be included in *Lineadinium* with other striate species. It has, however, the rotundity of species of the former subgenus, combined with the marked radial arrangement of the internal metaplasmic structures, so generally developed in *Pachydinium*. It is the most finely striate species in the genus *Gymnodinium*.

## **Gymnodinium ravenescens** sp. nov.

Plate 1, figure 10; text figure X, 21

DIAGNOSIS.—This is a small species with ellipsoidal body, its length 1.47 transdiameters; girdle premedian, displaced three times its own width; sulcus extending from apex to antapex; olive ochre chromatophores. Length, 53μ. Pacific off La Jolla, California, August.

DESCRIPTION.—The body is symmetrically ellipsoidal with broad, rounded apices, its length 1.47 transdiameters at the widest part. A cross-section of the body is nearly circular with a slight indentation on the midventral surface. The length of the hypocone is greater than that of the epicone by 0.27. The transdiameters of both are subequal. The epicone is hemispherical anteriorly, the sides slightly elongated posteriorly. The apex is broad and rounded. It has a length on the left and right sides of 0.31 and 0.49 respectively of the total length of the body.

The posterior half of the hypocone is a smoothly rounded hemisphere. The sides of the anterior half are subparallel.

The girdle is premedian in position, its proximal end meeting the sulcus at a distance from the apex of 0.31 and its distal end 0.49 respectively of the total length of the body. Its course around the body is that of a descending left spiral with the distal end displaced posteriorly about three times its own width. The furrow is wide, about 0.08 transdiameter, and is deeply impressed, its sides gradually curving outward to meet the surface of the body. The distal end of the furrow is somewhat narrower than the proximal. The sulcus begins near the apex and extends to the antapex in a slightly sinuous course. The trough is relatively shallow and fades out near both apices. Posterior to the proximal junction with the girdle the furrow becomes narrow and again below the distal junction it contracts to about half the width anteriorly. Beyond the posterior pore it widens and deepens, but soon fades out without reaching the antapex. The anterior flagellar pore is found at the anterior junction of girdle and sulcus, the posterior pore midway between the distal junction and the antapex.

The nucleus is an ellipsoidal body, closely filled with fine, moniliform, chromatin strands. These follow its long axis which lies parallel with the major axis of the body. It lies in the left side of the hypocone, quite close to the surface. The major and minor axes of the nucleus are 0.58 and 0.41 transdiameters in length respectively.

A small sacklike pusule opens into each flagellar pore. The cytoplasm is very clear and transparent, its very finely granular structure scarcely evident. Minute green spherules, oil droplets, and a few refractive granules are scattered through it. A single large vacuole, clear grey in color, was found on the right side near the junction of girdle and sulcus. This was slightly irregular in outline and had the appearance of a food body. Another smaller body of the same color was present in the epicone. The cytoplasm is pearl grey in tone. The general color of the organism is given to it by the small, flat, ellipsoidal chromatophores scattered profusely through the cytoplasm. These are olive ochre in color and are found near the center of the cytoplasm as well as near the periphery.

Dimensions.—Length, 53$\mu$; transdiameter, 36$\mu$; axes of nucleus, 21$\mu$ and 15$\mu$.

Occurrence.—A single individual was taken August 6, 1917, with a No. 25 net, 4 miles off La Jolla, California, in a haul from 60 meters to the surface in a surface temperature of 21°2 C.

Comparisons.—This is one of the few pelagic species of *Gymnodinium* which shows the presence of distinct chromatophores. The other pelagic species with chromatophores found by us include *G. cinctum* and *G. herbaceum*. Chromatophores are a quite common characteristic of the minute forms inhabiting the sand beach, such as *G. agile*, *G. flavum*, and most species of *Amphidinium*, and are also general among the fresh-water species. It is near *G. fuscum* in proportions, but is more rotund posteriorly, smaller and more olivaceus. It approaches *Gyrodinium ovoideum* in form of girdle.

## **Gymnodinium rete** Schütt

Text figure BB, 16

*Gymnodinium rete* Schütt (1895), p. 43, pl. 26, fig. 89.

Description.—Under this name Schütt (1895) figures an organism with an elongated, cylindrical body; girdle on the left side of the body only, with a groove extending anteriorly from its proximal end; nucleus spheroidal, filled with chromatin granules; yellow ochre chromatophores; broad pseudopodium-like flagellum (?) extending from the girdle at the left lateral margin of the body.

This is a problematical organism and one which it is difficult to locate systematically with the existing data. It presents no *Gymnodinium* characteristics unless we consider it a mutilated form. The extension on the girdle over half the ventral face would point towards *Hemidinium* for its affinities, rather than towards *Gymnodinium*. Until it has been redescribed, however, it must be left among the species *incertae sedis*. Its condition indicates approaching cytolysis, and its structure suggests that its anteroposterior orientation has been reversed.

## **Gymnodinium rhomboides** Schütt

Text figure Y, 15

*Gymnodinium rhomboides* Schütt (1895), p. 163, pl. 21, fig. 63.
*G. rhomboides*, Lemmermann (1899), p. 358.
*G. rhomboides*, Paulsen (1907), p. 23; (1908), pp. 97, 99, fig. 136. After Schütt (1895).
*G. rhomboides*, Doflein (1909), p. 461, fig. $412_{1-2}$; (1911), p. 527, fig. $472_{1-2}$. After Schütt (1895).
*G. rhomboides*, Lebour (1917*b*), pp. 183, 190, 191, fig. 6. In part, includes *G. fissum*.

Diagnosis.—A small species with symmetrical biconical body, its length 1.76 transdiameters; girdle displaced twice its own width; sulcus extending from near the apex to a short distance from the antapex; surface ridged. Length, 46μ. Atlantic or Mediterranean at Naples, Skagerak, and Plymouth Sound, England.

Description.—The body is biconical or rhomboidal in shape, widest at the middle, its length 1.7 transdiameters. The epicone and hypocone are both symmetrically cone-shaped (about 60°) with rounded apices. The hypocone exceeds the epicone in length by about 0.13 of its own length. The epicone has a length on the left and right sides of the sulcus of 0.47 and 0.57 respectively of the total length of the body.

The girdle joins the sulcus proximally about 0.47 and distally 0.57 of the total length of the body from the apex. It is slightly premedian in position as a whole. It has a width of about 0.09 transdiameter and is deeply impressed with overhanging borders. The sulcus invades the epicone slightly more than midway between girdle and apex and extends posteriorly to a short distance from the antapex as a slightly sinuous line. The anterior flagellar pore is found at the proximal junction of the girdle and sulcus and the posterior pore near the distal end of the sulcus.

The nucleus is a small spheroidal body, centrally located. Its diameter is about 0.4 transdiameter in length. The cytoplasm is filled with minute spherules of various sizes, most numerous in the epicone and near the antapex. The surface is ribbed with faint longitudinal furrows (?), about fifteen across the dorsal face, which are distinct near the girdle and fade out near the apices.

Dimensions.—Length, 46μ; transdiameter, 26μ; diameter of nucleus, 12μ.

Occurrence.—This species was figured by Schütt (1895) from the collections of the Plankton Expedition from the Bay of Naples or from the Atlantic. It has been recorded from the Skagerak by Paulsen (1907) and from Plymouth Sound, England, by Lebour (1917*b*).

Comparisons.—The marked biconical symmetry of the epicone and hypocone, combined with the striate surface, distinguish this species, at once, from all others in the genus. It has somewhat the same size and proportions as *G. scopulosum* sp. nov. (fig. X, 6), but is less rotund and has striae, or at least linear markings, due to modifications on or in the surface layer of cytoplasm.

### **Gymnodinium roseolum** (Schmarda) Stein

Text figure BB, 11

*Glenodinium roseolum* Schmarda (1854), p. 12, pl. 1, fig. 9.
*G. roseolum,* Leuckart (1861), p. 256. Based on Schmarda (1854).
*G. roseolum,* Diesing (1866), p. 105.
*G. roseolum,* Stein (1878), p. 73, as *Gymnodinium roseolum,* p. 90.
*Gymnodinium roseolum,* Eyferth (1879), p. 19.
*Peridinium roseolum,* Maggi (1880*a*); *Glenodinium roseolum* (1880*b*), p. 12.
*Gymnodinium roseolum,* Saville-Kent (1880–82), p. 444, pl. 25, fig. 53. Based on Schmarda (1854).
*Glenodinium roseolum,* Bütschli (1885), pp. 965, 1018.
*G. roseolum,* Entz (1888)), p. 41; as *Gymnodinium roseolum,* (1902), p. 124; (1907), p. 17; (1909), p. 253.
*Gymnodinium roseolum,* Schilling (1891*b*), pp. 199, 206. *Lapsus.*
*Glenodinium roseolum,* Schewiakoff (1893), p. 157.
*G. roseolum,* Lemmermann (1900), p. 118.

Diagnosis.—A minute species with ovoidal body, its length 1.28 transdiameters; girdle premedian; color pale pink. Fresh water in Egypt, February.

Description.—The body is ovoidal, widest near the middle, its length 1.28 transdiameters at the widest part. The epicone is about 0.5 the length of the hypocone and 0.68 its greatest width, with rounded outline. The hypocone is rounded anteriorly, subconical (about 63°) posteriorly, with blunt apex.

The girdle is premedian in position, its distance from the apex being about 0.3 the total length of the body. It is narrow and deeply impressed. The sulcus, flagella and nucleus were not observed by Schmarda (1854), the only cell inclusions being one red and several green spherules (chlamydomonads). The general color is pale pink. It is apparently holozoic in nutrition.

Dimensions.—Length, 38$\mu$; transdiameter, 29.5$\mu$.

Occurrence.—It was figured by Schmarda (1854) from the Natron Sea in Egypt in February.

Comparisons.—Schmarda's description is rather inadequate, but since the form figured is quite unlike any other species of *Gymnodinium* it seems best to let it stand until further work shall complete the description. Its shape, proportions, and size are near those of *G. cinctum* sp. nov. (fig. X, 28), a marine species, but its color differs, being pink instead of ochraceous. The color is unusual in fresh-water species.

Synonymy.—It was figured by Schmarda (1854) as *Glenodinium roseolum,* but it was later changed by Stein (1878) to *Gymnodinium.*

### **Gymnodinium rotundatum** Klebs

Text figure X, 8

*Gymnodinium rotundatum* Klebs (1912), pp. 392, 403, 439, fig. 5.
*G. rotundatum,* Cavers (1913), p. 182, fig. $9_{3-8}$.
*G. rotundatum,* Schilling (1913), p. 16, fig. 13.

Diagnosis.—A small species with rounded subellipsoidal body, its length 1.1 transdiameters; girdle without displacement; sulcus extending from girdle to antapex; yellow chromatophores. Length, 34µ. Fresh-water swamps near Vernheim, Germany.

Description.—The body is stout ellipsoidal, its length 1.1 transdiameters at the widest part. The epicone and hypocone are subequal in length. The epicone is hemispherical in shape, the left side more convex than the right. Its length is about 0.5 the total length of the body. The hypocone is broadly rounded with the antapex obliquely concave on the left side.

The girdle is submedian in position and forms a complete circle about the body. Its distance from the apex is about 0.5 of the total length of the body. The furrow is wide, about 0.1 transdiameter, and deeply impressed. The sulcus extends from the girdle to the antapex as a wide furrow. The position of the flagellar pores is not indicated in Klebs's (1912) figures.

The nucleus is a small spherical body in the central part of the organism. Its diameter is about 0.29 transdiameter in length. Numerous yellow rod-shaped chromatophores are radially arranged in the peripheral zone of the cytoplasm.

Dimensions.—Length, 32–35µ; transdiameter, 22–25µ; diameter of nucleus, 4µ. In Klebs's (1912, fig. 5*c*) figure, however, the dimensions are 34µ by 30µ, and we have followed this in the figure and description given herewith, rather than distort his figure to conform to the dimensions given in his text.

Occurrence.—This species has been described by Klebs (1912) from fresh-water swamps near Vernheim (Reid, Hessen), Germany, and has not been noted elsewhere.

Comparisons.—This species is near *G. uberrimum* in proportions, but is somewhat more rotund anteriorly and less symmetrical posteriorly. Its chromatophores resemble those of *G. mirabile* and *G. uberrimum* in being rodlike and radially arranged. It is also near *G. bogoriense* of the same author (Klebs, 1912), from Java, but the latter is smaller and more regular in outline.

### **Gymnodinium rubricauda** sp. nov.

Plate 8, figure 88; text figure X, 4

Diagnosis.—A medium sized species with subovoidal body, its length 1.25 transdiameters; girdle submedian, without displacement; sulcus extending from apex to antapex; color, rose red. Length, 69µ. Pacific off La Jolla, California, July, August.

Description.—The body is subovoidal, widest posteriorly, tapering anteriorly, its length 1.25 transdiameters at the widest part. In cross-section the body is nearly circular with a deep

trough down the ventral face. The lengths of the epicone and hypocone are about equal, but the hypocone, having a continuously wider transdiameter, exceeds the epicone in size. The epicone has the shape of a cone of about 70° with a blunt, rounded apex. The sides form almost straight lines from the apex to the girdle. The middle third of the ventral face is deeply concave, forming a trough in the bottom of which lies the sulcus. This becomes shallow anteriorly, fading out at the apex. The length of the epicone is about 0.49 of the total length of the body. The hypocone is truncate-pyramidal in outline and is less symmetrical than the epicone. The sides are concave-convex and form angles of about 25° with the longitudinal plane of the body. The antapex is broad, about half the greatest diameter of the body, and is truncated by the broad sulcal notch.

The girdle is submedian in position, its distance from the apex being 0.49 of the total length of the body. It forms a complete circle about the body, the ends meeting without displacement. The furrow has a width of about 0.08 transdiameter and is deeply impressed. The anterior lip is deeply undercut, the posterior side of the furrow gradually rounding out to the surface of the body. The borders of the girdle are smooth.

The sulcus extends from the apex to the antapex in a slightly sigmoid curve. It lies at the bottom of a broad trough which indents the ventral face of the body. It is narrow, expanding beyond the posterior flagellar pore both laterally and in depth, forming a broad notch at the antapex. The anterior flagellar pore opens at the junction of the girdle and sulcus. The transverse flagellum traverses 0.95 of the entire length of the girdle. The posterior flagellar pore is found slightly beyond the midpoint between the girdle and the antapex.

The nucleus is a large, spheroidal body filled with moniliform chromatin strands. It is found on the left side of the body slightly anterior to the equatorial plane. Its axis is about 0.47 transdiameter in length.

The cytoplasm is very finely granular, clear and transparent. Sacklike pusules are usually present at either or both pores. Nutrition is holozoic, indicated by the presence of food bodies in the cytoplasm. In the individual figured two food bodies were present. One was a large grey-green, spheroidal body on the right side near the nucleus, the other was an irregular mass in the posterior part of the body, mustard yellow in color. The general color of the organism is rose red diffused through the cytoplasm. This is strongest in the epicone and near the periphery, with more neutral pearl-grey tone in the hypocone. In the antapical region the coloring matter or pigment is condensed into a few, very small, rose-red granules. A group of larger granules of the same color can be found in the apex. No striae or other surface markings could be detected.

Dimensions.—Length, 68–85$\mu$; transdiameter, 54–69$\mu$; axis of nucleus, 20–27$\mu$.

Occurrence.—This was first met with July 18, 1917, in a haul taken with a No. 25 silk net, 4 miles off La Jolla, California, from 80 meters to the surface and in a surface temperature of 20°8 C. It was found in most of the hauls taken between that date and August 21, both in the surface hauls at the end of the pier at the Biological Station and in those made farther offshore. It was most abundant towards the end of that time, sixteen individuals being counted in the last haul examined.

Comparisons.—This species belongs to a color group which has representatives also in *Gyrodinium, Cochlodinium, Pouchetia,* and *Erythropsis,* characterized by various shades of red. This group is represented in *Gymnodinium* by *G. sulcatum, G. rubrum,* and *G. contractum,* all of which show the same shade of rose red. This is repeated also in *Cochlodinium rosaceum.* In *Gyrodinium*

the color shades from dahlia purple in *G. postmaculatum* to coral red in *G. corallinum*. In *Pouchetia* the color in this group varies from amaranth purple in *P. purpurescens* to dahlia purple in *P. purpurata* and spinel red in *P. voracis*.

*Gymnodinium rubricauda* belongs in the subgenus *Gymnodinium*, as do most of the species with colored pigment in the genus. It belongs to the group, in the subgenus *Gymnodinium*, which includes *G. sulcatum* and *G. contractum*, in which the differences are mainly in proportions, distribution of the color, and the extent of the sulcus. The sulcus extends from apex to antapex in *G. sulcatum* and *G. rubrum* (figs. X, 1; Y, 4), but is confined to the hypocone in *G. contractum* (fig. X, 2). In addition to these peculiarities the surface of *G. rubricauda* is entirely devoid of striae, while feeble markings occur on the hypocone of *G. sulcatum* and on the epicone of *G. contractum*. In view of the number of individuals conforming to these differences, seen in the case of *G. sulcatum* and *G. rubricauda*, we conclude that they are not phases of one and the same species.

### **Gymnodinium rubrum** sp. nov.

Plate 8, figure 86; text figures A, Y, 4

DIAGNOSIS.—This is a large species with ovoidal body, its length 1.81 transdiameters; girdle submedian, descending left spiral, displaced 0.37 transdiameter; sulcus extending from apex to antapex in a sinuous course; surface striate; color pale glaucous green and rose red; remarkably labile in form. Length, 145μ. Pacific off La Jolla, California, July, August.

DESCRIPTION.—The body is quite labile and variable in shape, normally ovoidal, circular in cross-section, widest anteriorly, with broad, rounded apices, its length 1.81 transdiameters at the widest part. Individuals showing great metabolic changes and distortions are frequently met with (fig. A). These variations include rounded-up forms and larger ones with deeply lobed apical or antapical ends. The epicone and hypocone are subequal in length, but the usually greater transdiameter of the epicone increases its relative size slightly. The epicone is rounded to conical in shape with broad apex. It has a length on the left and right sides of 0.4 and 0.59 respectively of the total length of the body. The hypocone is more asymmetrical than the epicone with greater irregularity in its outline. The antapex is broad and rounded and more or less deeply notched by the distal end of the sulcus.

The girdle is submedian in position, its proximal end joining the sulcus at a distance from the apex of 0.4 and its distal end at 0.59 of the total length of the body. It follows a descending left spiral course around the body with a posterior displacement of its distal end of 0.37 transdiameter and with an overhang of about 0.01 transdiameter. The furrow is wide, about 0.06 transdiameter, and deeply impressed, its overhanging borders raised considerably above the surrounding surface of the body.

The sulcus usually begins at or near the apex and extends posteriorly to the antapex. It follows a slightly sinuous course on the epicone and is deflected sinistrally at an angle of about 20° below the anterior junction with the girdle. After passing the distal junction it again assumes a nearly longitudinal direction and continues thus to the antapex. Throughout its course it occupies a deep trough which widens to twice its anterior transdiameter beyond the

proximal junction with the girdle, narrows somewhat at the distal junction and expands and deepens near the posterior part of the body. The anterior flagellar pore is found at the proximal junction of the girdle and sulcus and the posterior pore about 0.18 transdiameter below the distal junction.

The nucleus is ellipsoidal and is found near the proximal end of the girdle on the left side of the body. It is composed of two distinct regions: an inner region which is granular or may exhibit moniliform chromatin strands, and surrounding this a zone which exhibits no differentiating structure. This zone has a width of about 0.17 transdiameter and has a double-contoured outer membrane. In one case it seemed to have the vacuolate structure similar to that found in the nucleus of *Gyrodinium corallinium* (pl. 10, fig. 117). The major and minor axes of the nucleus are 0.4 and 0.3 transdiameters in length respectively.

A sacklike pusule is usually present at the anterior flagellar pore. In some individuals it was present at both pores. The cytoplasm is remarkably clear and transparent. Among all the specimens observed very few possessed cell inclusions, such as food masses and oil globules. Many were seen, however, with what appeared to be a food vent at the posterior end of the body, as if a large food mass had been recently ejected. The color of the cytoplasm is pale diffused rose red at the anterior end, shading posteriorly to pale sea-foam yellow or pale glaucous green. These colors are strongest at the apices and appear to be diffused through the cytoplasm. Minute granules of rose red pigment are usually present in the periphery of the body, strung along the surface striae like beads on a string. These are most numerous at the apex and girdle, the largest granules being found along the proximal border of the girdle. On the hypocone they are scattering, few in number, and widely separated.

The surface is striate, with longitudinal, equidistant lines. The number of lines on the epicone is about half that on the hypocone. They are clear greenish yellow, and may be continuous or may be composed of short, broken dashes.

DIMENSIONS.—Length, 100–145$\mu$; transdiameter, 75–90$\mu$; axes of nucleus, 35–37$\mu$ and 25–27$\mu$.

OCCURRENCE.—This species was found abundantly in most of the hauls made between July 11 and August 22, 1917, and was present in surface hauls as well as those made from 80 meters to the surface, and at distances offshore varying from the end of the pier at the Biological Station at La Jolla, California, to 10 miles.

COMPARISONS.—This species is unique in the genus *Gymnodinium* in possessing a nucleus composed of two distinct parts. This was found in all the individuals observed and thus could not be a temporary condition characteristic of some particular stage in the life history. Dividing forms, however, were notably absent in all the material under observation. The same type of nucleus is present in *Gyrodinium corallinum* and *G. virgatum*. Here, again, the appearance of the dividing nucleus was not observed.

It belongs to the subgenus *Lineadinium*, but the degree of displacement of the girdle and torsion of the body bring it close to the genus *Gyrodinium*. The similarity of its nucleus to that of certain species in that genus strengthen the relationships. It is on the border line between the genera *Gymnodinium* and *Gyrodinium*, and might be included in either without violence to its structural revelations.

It is near *Gymnodinium lineatum* sp. nov. (fig. Y, 14), but differs in its surface markings, form of hypotheca, and lability.

## **Gymnodinium scopulosum** sp. nov.

Plate 1, figure 7; text figure X, 6

Diagnosis.—A small species with obovoidal to subbiconical body, its length 1.8 transdiameters; girdle submedian in position, displaced 0.3 transdiameter; sulcus extends from near apex to antapex; color, oil yellow. Length, 47μ. Pacific off La Jolla, California, August.

Description.—The body is obovoidal, widest anteriorly, tapering slightly at both apices which are rather broad, its length 1.8 transdiameters at the widest part. The epicone exceeds the hypocone in length by 0.11 of its own length, and in transdiameter by 0.21 of its own transdiameter. It forms an overhanging, craglike dome with rounded sides and slightly tapering apex. It has a length on the left and right sides of 0.4 and 0.56 respectively of the total length of the body. The hypocone is more slender than the epicone, tapering more posteriorly with a narrow antapex.

The girdle is submedian in position. Its proximal end joins the sulcus at a distance from the apex of 0.4 of the total length of the body. It passes around the body in a descending left spiral course, its distal end meeting the sulcus at a distance from the apex of 0.56 of the total length of the body, displaced 0.3 transdiameter. The furrow has a width of about 0.09 transdiameter and is deeply impressed, undercutting the anterior border and smoothly curving out to the posterior one. The anterior border projects far out beyond the posterior border. The sulcus begins a short distance below the apex and extends posteriorly in an almost straight line to the antapex. The anterior flagellar pore opens at the proximal junction of the girdle and sulcus, the posterior pore midway between the distal junction and the antapex.

The nucleus is a small ellipsoidal body lying in the left side of the epicone. It is filled with coarse, moniliform chromatin strands following its longest diameter. Its major and minor axes are 0.53 and 0.36 transdiameters in length respectively.

A small sacklike pusule opens into each flagellar pore. The cytoplasm is very finely granular and contains few inclusions, such as vacuoles and food bodies. Near the posterior end of the nucleus one large pink vacuole and a number of small, blue-green ones were present in the epicone. The color of the cytoplasm presents a mixture of blue green, oil yellow, and pearl grey, with deeper tones of oil yellow on the sides and at both ends. A thin, hyaline cyst, considerably larger than the body, enclosed the organism.

Dimensions.—Length, 47μ; transdiameter, 26μ; axes of nucleus, 14μ and 9μ; length of cyst, 52μ; transdiameter of cyst, 38μ.

Occurrence.—Two individuals were taken August 6, 1917, in a haul 4 miles off La Jolla, California, from 60 meters to the surface and in a surface temperature of 21°2 C.

Comparisons.—This species belongs to the subgenus *Gymnodinium sensu strictu*, characterized by a thin periplast without surface markings. It is close to *G. lunula*, but is larger, has more tapering apices, greater disproportion of epicone and hypocone, and straighter sulcus. Nothing is known of "pyrocystis" stages of this species.

### **Gymnodinium simplex** (Lohmann) Kofoid and Swezy

Text figure BB, 8

*Protodinium simplex* Lohmann (1908), pp. 264, 265, pl. 17, fig. 17; (1911), pp. 23, 30, 31, fig. 12.
*P. simplex,* Schiller (1911), p. 31.
*P. simplex,* Ostenfeld (1913), p. 339.

Diagnosis.—This is a minute species with broadly ellipsoidal body, its length 1.53 transdiameters; girdle median, a closed circle; sulcus absent (?); yellow, leaflike chromatophores. Length, 20μ. Baltic Sea near Kiel, Germany, throughout the year.

Description.—The body is broadly ellipsoidal with broad apices, circular in cross-section, its length 1.53 transdiameters at the widest part. The girdle is poorly defined in Lohmann's figure (our text figure BB, 8), but seems to be median in position, dividing the body into two subequal parts, both subhemispherical in shape, with broad, rounded apices. His figure further lacks flagella and pores as well as any indication of a sulcus. The latter structures he notes as absent.

The nucleus is a relatively large body centrally located and filled with chromatin granules. Its diameter is about 0.6 transdiameter of the body in length. Yellow, leaflike chromatophores are arranged in the periphery of the cell. These vary from four to many in number.

Dimensions.—Length, 10–20μ; transdiameter, 13μ; diameter of nucleus, 8μ.

Occurrence.—Described by Lohmann (1908) from the Baltic Sea near Kiel, Germany, where it occurred throughout the year, sparingly in the winter and reaching its maximum in July.

Synonymy.—This species was described by Lohmann as *Protodinium simplex*, thus creating for it a new genus without, however, a full statement of his reasons for so doing. The lack of a definite sulcus cannot well be used as a generic distinction, since this structure, as well as the girdle, is sometimes lacking in Lohmann's figures of other species, as well as in those of many earlier biologists. It possesses only the characters of the girdle, hypocone, and epicone, which identify it with the group of minute *Gymnodinium*, and we therefore place it in that genus, discarding Lohmann's new genus, *Protodinium*, pending a full reëxamination of these details. In the event that there is no trace of the sulcus prior to cytolysis, the genus *Protodinium* might well stand and be transferred to the Protodiniferidae. Our reluctance to place it there now is based on our experience with living, naked dinoflagellates in crowded plankton collections, such as those with which Lohmann evidently worked. The rounding up of the body under these conditions tends to obliterate the girdle and sulcus, and this may have been the case with the individuals on which Lohmann's figures and description are based.

### **Gymnodinium situla** sp. nov.

Plate 1, figure 12; text figure Z, 6

Diagnosis.—This is a medium sized species with rotund, cup-shaped body with conical epicone; its length 1.2 transdiameters; girdle submedian, displaced its own width; sulcus extending from apex to antapex; surface finely striate; color, pale dull green yellow. Length, 66$\mu$. Pacific off La Jolla, California, July, August.

Description.—The body is rotund, shaped somewhat like a cup with a high conical cover, widest in the girdle region, its length 1.2 transdiameters at the widest part. In cross-section the body is nearly circular with only a slight groove down the midventral surface. The hypocone exceeds the epicone in size, its length being subequal, but its wider transdiameter giving it a greater actual size. The epicone has the shape of a short cone of about 90°, with a broad base. The apex is blunt and the sides only slightly convex. It has a length of about 0.45 on the left and 0.50 of the total length on the right side. The hypocone is cup-shaped with a wide, flaring border at the girdle. The sides taper very slightly towards the posterior end which is broad and rounded, with the central part slightly notched by the distal end of the sulcus.

The girdle is submedian. Its proximal end joins the sulcus at a distance from the apex of about 0.45 and its distal end 0.50 of the total length of the body. It passes around the body in a nearly transverse direction with a slight deflection posteriorly on the right side, which displaces the distal end about one width of the girdle. The furrow is wide, about 0.09 transdiameter, and is deeply impressed. The lip on the proximal side is undercut, the distal side of the furrow gradually curving outward to the surface of the body. The borders are irregular in outline, following the slight undulations of the surface. The sulcus begins at the apex and extends posteriorly to the antapex. It occupies a narrow, deep trough which fades out at the apex. Beyond the posterior flagellar pore it becomes wider and deeper, extending through the body to the dorsal surface at the antapex, forming an excavation which deeply notches that part of the body. The borders of the sulcus are smooth in outline. The anterior flagellar pore is found at the proximal junction of the girdle and sulcus, the posterior pore midway between the distal junction and the antapex.

The nucleus is spheroidal and is found in the right side of the posterior half of the body. Its axis is about 0.3 transdiameter in length. A large sacklike pusule opens into the anterior flagellar pore, a more slender one into the posterior pore.

The cytoplasm is granular and finely alveolate in structure. This is omitted from the figures for the sake of clearness. A mass of large pink vacuoles occupies the major part of the epicone. A smaller group of pink vacuoles, very much smaller in size, is found near the antapex. Two large, spherical, ochraceous orange-colored bodies or vacuoles and one bluish one were located near the anterior pore. These were presumably food bodies in digestion. Behind these and closely grouped around the anterior pusule and on the right side of the sulcus was a mass of small, highly refractive bodies. These were citron yellow in color, and were evidently of a fatty nature. Nutrition is holozoic.

The entire surface of the organism is covered with fine, longitudinal, equidistant striae. These were composed of short blue-green dashes, linearly arranged. The number on the hypocone is about a fourth greater than on the epicone. There are about 30 striae at the girdle on the epicone. The surface of the body is roughened and irregular, presenting a similar outline to that shown in *G. pachydermatum*. In this form, however, the peripheral, alveolar zone of ectoplasm is not so clearly differentiated as in the other species. The general color of the organism is a pale, dull greenish yellow, shading to chalcedony yellow near the girdle and sulcus, the thickness of the body giving to the whole a rich effect.

Dimensions.—Length, 66μ; transdiameter, 55μ; axes of nucleus, 19μ and 15μ.

Occurrence.—One individual was taken July 26, 1917, with a No. 25 silk net, 2.5 miles off La Jolla, California, in a haul from 80 meters to the surface and in a surface temperature of 21°6 C. Another was taken August 17, with the same apparatus and from the same depth, 0.75 mile off La Jolla, and on August 21, in a haul 5 miles offshore and from 83 meters to the surface.

Comparisons.—This species belongs in the subgenus *Pachydinium* along with *G. dogieli* sp. nov., *G. amphora* sp. nov. (figs. AA, 6, 8), and other species characterized by a thickened periplast. There is less structural differentiation in that region in this species than in the remainder of the group. The slight undulations of the surface, particularly noticeable along the borders of the girdle, leave little doubt about the character of the layer of protoplasm immediately beneath, hence its inclusion with that subgenus. In the richness of its coloring and the cytoplasmic inclusions it resembles the larger species of that subgenus, notably *G. amphora* and *G. dogieli,* being unlike them, however, in having surface striae.

## **Gymnodinium sphaericum** Calkins

Plate 4, figure 42; text figure AA, 9

*Gymnodinium gracile* var. *sphaerica* Calkins (1902), p. 429, fig. 20.

Diagnosis.—This is a medium sized species with rotund, spheroidal body, very slightly flattened dorsoventrally, its length and transdiameter nearly equal or the length may be about 1.27 transdiameters; girdle premedian, displaced its own width or slightly more; sulcus short on the epicone, extending to antapex; color, amber yellow and olive ochre. Length, 60μ. Atlantic off Woods Hole, Massachusetts, and Pacific off La Jolla, California, July, August.

Description.—This is a medium to small species of robust habit, the body spheroidal to broadly ellipsoidal, with broad apices, its length and width almost equal or its length may reach 1.27 transdiameters. In cross-section the body shows a slight dorsoventral flattening. This, however, seems to be an unusual condition. The hypocone exceeds the epicone in size, its length being greater by 0.3. The epicone has an outline of something less than a hemisphere, with broad, smoothly rounded apex. It has a length on the left and right sides of 0.28 and 0.38 respectively of the total length of the body. The posterior half of the hypocone is hemispherical in shape, the sides of the anterior half being subparallel. The apex is broad and rounded. In figure 42, plate 4, the body is slightly distorted in outline as though from the result of pressure obliquely on the surface. Text figure AA, 9, gives a better outline of the normal individual.

The girdle is premedian in position, its distance from the apex at the proximal end being about 0.28 and at its distal end 0.38 of the total length of the body. Its path around the body is that of a descending left spiral, displaced posteriorly its own width or slightly more. The furrow is wide, about 0.06 transdiameter, and is deeply impressed. The anterior lip is undercut, the posterior side of the furrow gradually rounding out to the surface of the body. The borders of the girdle are marked by the undulations of the surface of the body or they may be smooth. The sulcus may invade the epicone only a short distance or may reach nearly to the apex. The anterior flagellar pore is located at the proximal junction of the girdle and sulcus, the posterior pore a short distance below.

The nucleus is an ellipsoidal body filled with coarse, moniliform chromatin strands. It is found in the anterior half of the body. Its major and minor axes are about 0.49 and 0.29 transdiameters in length respectively. The greatly elongated nucleus in figure 42, plate 4, is a predivision stage.

Small, sacklike pusules may open into either or both flagellar pores. The cytoplasm is very finely granular, clear and transparent. The body usually contains numerous food masses and small refractive granules. The presence of long, slender green rodlets is common in many individuals. In text figure AA, 9, the posterior part of the body is filled with a very large food body. Nutrition is holozoic. A distinct ectoplasm can be observed in most of the specimens. This is most conspicuous on the surface which exhibits the same undulations found in *G. pachydermatum*. The general color of the organism is pale cendre green shading to yellow ochre. No striae or other markings could be detected on the surface.

Dimensions.—Length, 47μ to 68μ; transdiameter, 40μ to 47μ; axes of nucleus, 10μ and 10μ.

Occurrence.—This was figured by Calkins (1902) from the Atlantic off Woods Hole, Massachusetts, July, August. It was first seen in the Pacific at La Jolla, California, July 18, 1906, in a surface haul made with a No. 20 net. On July 20 it was again taken under the same conditions. During July and August, 1917, it was frequently met in the surface hauls made at the end of the pier at the Biological Station and in a number of the deep hauls made farther offshore. The number of individuals observed in one haul varied from one to three. A thin, double-contoured cyst enclosed many of them when first observed. In one specimen noted two individuals were enclosed in one cyst, probably the resulting products of division.

Comparisons.—This species belongs in the subgenus *Pachydinium* because of the presence of a thickened ectoplasm. Its color, greenish yellow, is that common to many of the species in that subgenus. It does not, however, show the highly differentiated ectoplasmic structure found in *G. pachydermatum* sp. nov. (fig. AA, 5), but more nearly approximates the condition in *G. situla* sp. nov. (fig. Z, 6) and, perhaps, *G. tenuissimum* sp. nov. (fig. AA, 7). Its smaller size and rotund ovoidal body clearly distinguish it from other species.

Synonymy.—This species was figured by Calkins (1902) as *G. gracile* var. *sphaerica*. It differs from *G. gracile*, however, in its lack of surface striae, size, proportions, and in its type of ectoplasmic differentiation, and is thus specifically distinct rather than subspecifically.

## **Gymnodinium sulcatum** sp. nov.

Plate 8, figure 83; text figure X, 1

Diagnosis.—A medium sized species with broad, rotund ovoidal body, its length 1.05 transdiameters; girdle submedian without displacement; sulcus extending from apex to antapex; hypocone sparsely ribbed; color, dull rose red. Length, 63μ. Pacific off La Jolla, California, August.

Description.—The body is rotund, its length and transdiameter nearly equal, widest at the middle, narrow anteriorly and broad posteriorly. In cross-section the body is nearly circular. The epicone and hypocone are subequal in size. The epicone is subconical in shape with an angle of about 80°. The sides are convex, the left one slightly sigmoid in outline, with scarcely

pointed apex. It has a length of 0.5 of the total length of the body. The hypocone is subhemispherical in shape, broadly notched at the antapex by the distal end of the sulcus. The left side is slightly sigmoid in outline, the right side nearly straight. The posterior end is bilobed in ventral view with two short, broadly rounded lobes.

The girdle is submedian and forms a complete circle around the body. Its distance from the apex is about 0.5 of the total length of the body. The furrow is wide, about 0.08 transdiameter and rather shallow, with smoothly rounded borders. The sulcus begins at the apex and extends posteriorly in a slightly sinuous line to the antapex. The furrow is narrow and lies in the middle of a wide trough which indents the ventral surface of the body. Posterior to the posterior pore it becomes wide and deep, reaching through the body to the dorsal surface, and forming a deep excavation at the antapex. The anterior flagellar pore is found at the proximal junction of the girdle and sulcus, the posterior pore midway between the girdle and antapex.

The nucleus is a spheroidal body found on the left side of the epicone. It is filled with moniliform chromatin granules. Its axis is about 0.33 transdiameter in length.

A large club-shaped pusule opens into each flagellar pore. The cytoplasm is very finely granular, clear and transparent. A single large, green yellow food mass was present near the nucleus. This was enclosed in a much larger food vacuole. The color of the organism is a dull rose red diffused throughout the cytoplasm. Near the apices particles of the coloring pigment were condensed into small globules of bright rose red color. These were slightly more numerous at the antapex than at the apex. On the surface of the hypocone are a number of ridges beginning below the girdle and extending posteriorly to near the antapex. These were four in number on the ventral face and six on the dorsal. They are yellow in color, narrow and raised slightly above the surface. None could be detected on the epicone. No other surface markings were present.

Dimensions.—Length, 63$\mu$; transdiameter, 60$\mu$; axis of nucleus, 20$\mu$.

Occurrence.—A single individual was taken August 6, 1917, with a No. 25 silk net 4 miles off La Jolla, California, in a haul from 60 meters to the surface and in a surface temperature of 21°9 C.

Comparisons.—This species and *G. contractum* and *G. rubricauda* have several features in common. The girdle forms a complete circle around the body and the general color is the same. Ridges are present on the epicone in *G. contractum* and are entirely absent in *G. rubricauda.* The enclosure of food bodies in a conspicuous vacuole is common to both *G. sulcatum* and *G. contractum.* The girdle is submedian in the three species. The possibility that these three are varieties of one species cannot be overlooked. However, many specimens of *G. contractum* and *G. rubricauda* were observed and these showed no intergradations of form. The solitary individual of *G. sulcatum* makes that species a more doubtful one.

## **Gymnodinium tenuissimum** Lauterborn

Text figure AA, 7

*Gymnodinium tenuissimum* Lauterborn (1894), pp. 391, 396; (1898), p. 388, pl. 18, fig. 26; (1910*a*), p. 464; (1910*b*), p. 499; (1913), p. 906.

*G. tenuissimum,* Lemmermann (1900), p. 116; (1902), p. 260; (1910), pp. 565, 618, 621, fig. 21.

*G. tenuissimum,* Zschokke (1900), p. 43.

*G. tenuissimum,* Lang (1901), p. 25, fig. 41.

*G. tenuissimum,* Schilling (1913), p. 18, fig. 17.

DIAGNOSIS.—A medium sized species with dorsoventrally compressed, discoidal body, its length 1.1 transdiameters; girdle without displacement; sulcus short. Length, 60μ. Fresh-water ponds near Maudach, Germany, through the winter months.

DESCRIPTION.—A medium sized species with disklike body, flattened dorsoventrally to a thin plate, its length 1.1 transdiameters. The hypocone exceeds the epicone in length by about 0.2 of its own length. In ventral view the epicone is subhemispherical with the right side of the semicircle longer than the left. Its length is about 0.4 of the total length of the body in the midventral region. The girdle curves posteriorly on the dorsal side, turning anteriorly before reaching the midventral region, giving the right side of the epicone at the edge of the disk a length of 0.5 the total length of the body. The hypocone is asymmetrical with a blunt antapex, longer upon the right side.

The girdle, as well as the sulcus, is incomplete in Lauterborn's (1898) figures. Its distance from the apex in the midventral region is about 0.4 of the total length of the body. It makes a posterior sweep on the dorsal side of the body, turning anteriorly in the last quarter of its course to the neighborhood of its origin. The furrow is rather deeply impressed, about 0.07 transdiameter in width, with sharply marked borders. The sulcus is only faintly indicated by a short line on the hypocone. The transverse and longitudinal flagella apparently take origin at points not far distant from the junction of the girdle and sulcus.

The nucleus is ellipsoidal and located in the central region of the body. It is filled with coarse chromatin granules. Its major and minor axes are 0.3 and 0.2 transdiameters in length respectively. The cytoplasm is filled with spherules of various sizes, and rounded, yellow-brown chromatophores.

DIMENSIONS.—Length, 66μ; transdiameter, 60μ; axes of nucleus, 19μ and 14μ.

OCCURRENCE.—This was figured by Lauterborn (1894, 1899) from fresh-water ponds near Maudach and Ludswigshafen, Germany, through the winter months.

COMPARISONS.—This species is tentatively allocated in the subgenus *Pachydinium* because of its differentiated peripheral cytoplasm, marked by radial structures. Lauterborn (1898) explicitly notes a clearly marked alveolar layer, but does not give its location. There is no other species in the genus approaching *G. tenuissimum*. The describer calls attention to its similarity to *Glenodinium foliaceum*, a flattened thecate species of the Peridinioidea.

## Gymnodinium tintinnicola Lohmann

Text figure BB, 13

*Gymnodinium tintinnicola* Lohmann (1908), pp. 259–260, 266, 366, pl. 17, fig. 6*a-c*.

The probability that some of the minute *Gymnodinium* found in the plankton are swarm spores of parasitic species belonging, it may be, to other genera has been demonstrated by Lohmann's discovery of a minute species which he has named *G. tintinnicola*. He found this organism emerging as a parasite from *Tintinnopsis nuclela*, one of the lorica-forming ciliates of the marine plankton. There were about ten of these "spores" in the ciliate. They have, in the free state, the typical form of *Gymnodinium* with the two characteristic flagella, the

trailing longitudinal one and the ribbon-like transverse one, and travel in the normal rotating fashion. There is apparently a sulcus and a postmarginal sulcal notch. No determination of the dinoflagellate nature of the nucleus was made. The organism was colorless, about 18$\mu$ in length and of nearly the same width.

Somewhat similar "spores" with girdle and sulcal notch were previously described by Lackmann (1906) as macrospores of *Tintinnopsis campanula* and *Cytharocytis helix*. Lohmann (1908) justly criticizes this interpretation and, correctly in our opinion, regards it as wholly improbable that a cilitate protozoan would have a dinoflagellate macrospore. The spores figured by Lackmann (1906, pl. 1, figs. 17–21) have a different appearance from those of Lohmann. They are larger and taper more anteriorly.

It may well be that Brandt's (1905) report that the swarm spores of the Radiolaria are of the dinoflagellate type is based upon observations of parasitic dinoflagellates and not radiolarian swarm spores. More evidence is essential before this subject can be set forth in its correct relations. In the meantime we leave Lohmann's species tentatively in *Gymnodinium*. It will, in all probability, find its place ultimately among the Blastodiniidae or other parasitic representatives of the dinoflagellates.

## **Gymnodinium translucens** sp. nov.

Plate 2, figure 17; text figure Y, 2

Diagnosis.—A medium sized species with ellipsoidal body, its length 1.93 transdiameters; girdle submedian, displaced about twice its own width; sulcus extending from apex to antapex; surface sparsely striate; color, bluish glaucous, very hyaline. Length, 87$\mu$. Pacific off La Jolla, California, June.

Description.—The body is slender ellipsoidal, pointed anteriorly, truncate posteriorly, its length 1.93 transdiameters at the widest part. A cross-section of the body is nearly circular with the midventral surface slightly indented. The epicone exceeds the hypocone in size, its length being greater by 0.14. Its transdiameter is also slightly larger. It is dome-shaped with high rounded sides and a short, sharply pointed apex. It has a length on the left and right sides of 0.51 and 0.60 respectively of the total length of the body. The sides of the hypocone are less convex than those of the epicone. Posteriorly it is deeply emarginate by the sulcal notch, with the two lobes broad and rounded.

The girdle is submedian in position. Its proximal end joins the sulcus at a distance from the apex of 0.51 and its distal end 0.60 of the total length of the body. The furrow is wide, about 0.09 transdiameter, and deeply impressed, with the sides gradually curving out to the surface of the body. The borders are marked by a double-contoured line, slightly crinkled and blue green in color. The sulcus extends from the apex to the antapex in a slightly sinuous line. It is very narrow and rather shallow on the epicone, expanding about three times this width beyond the anterior flagellar pore. After passing the distal end of the girdle it becomes much wider and sinks deeper into the body until, near the antapex, it reaches the dorsal surface, bifurcating the posterior part of the body. The two lobes are broad and rounded. The anterior flagellar pore opens at the proximal end of the girdle, near the place of union with the sulcus. The posterior pore is slightly beyond the distal junction of girdle and sulcus.

The nucleus is a rather large, spheroidal body filled with fine chromatin strands. It is found in the left dorsal side of the hypocone. Its axis is about 0.44 transdiameter in length.

The cytoplasm is very clear and transparent and without apparent granulations. It is suffused throughout with a glassy, bluish glaucous tint which gives its color to the organism. The anterior half of the body contains a large food mass, irregular ellipsoid in shape and greyish javel green in color. Two smaller, grey, refractive bodies were present in the hypocone, and a number of still smaller refractive bodies in the antapical region near the nucleus. Nutrition is evidently holozoic. The surface is covered with longitudinal, equidistant striae, blue green in color, about 20 across the ventral face of the girdle. The number of these on the hypocone exceeds the number on the epicone by about 0.1.

DIMENSIONS.—Length, 87$\mu$; transdiameter, 45$\mu$; axes of nucleus, 25$\mu$.

OCCURRENCE.—A single individual was taken June 26, 1917, at La Jolla, California, with a No. 12 net, 1 mile offshore, in a haul from 120 meters to the surface and in a surface temperature of 20°6 C.

COMPARISONS.—This form has the glassy, glaucous appearance not uncommon throughout the Gymnodiniidae, as, for example, in *Cochlodinium vinctum* and *Erythropsis extrudens*. *Gymnodinium gracile* sometimes exhibits the same bluish color, but the two species are widely different in their morphological characters. It belongs to the subgenus *Lineadinium*, but stands rather alone. Its epicone and general form approach that of *G. multilineatum* sp. nov. (fig. Y, 18), but its bifid antapex, sparse striae and displaced girdle clearly separate it from that species.

## Gymnodinium triangularis Lebour

Text figure BB, 2

*Gymnodinium triangularis* Lebour (1917*b*), p. 192, fig. 7.

The form figured by Lebour (1917*b*) as *G. triangularis* is evidently a mutilated specimen. The posterior part of the body is frequently deformed in many of these frail, delicate organisms, as in *Pouchetia maxima* (pl. 6, fig. 61). This is often the result of the extrusion of a large food mass, and the deformation may last for some time or may close immediately. This process was often followed by us, particularly in *Gymnodinium heterostriatum*.

The form figured by Lebour is subtriangular in shape, truncate posteriorly, with the hypocone greatly exceeding the epicone in size. The sulcus is omitted from the figure, but the longitudinal flagellum arises near the apex (?). The data given are incomplete, and, combined with the reasons stated above, would throw this among the doubtful forms until it has been found again. The point of origin of what is apparently the longitudinal flagellum raises the question of the orientation of this organism, which may possibly be inverted.

### **Gymnodinium uberrimum** (Allman) Kofoid and Swezy

Text figure X, 9

*Peridinium uberrima,* Allman (1854), pp. 118–120; (1855), pp. 24–25, pl. 3, figs. 9–17.
*Melodinium uberrimum,* Saville-Kent (1880–82), pp. 445–446, pl. 25, figs. 34–35.
*Gymnodinium mirabile* var. *rufescens* Penard (1891), pp. 34, 57, pl. 5, figs. 8–9.
*G. mirabile rufescens,* Imhof (1892), p. 175.
*G. rufescens,* Lemmermann (1900), p. 116; (1902), p. 260; (1910), p. 565, figs. 17, 18, pp. 623–624.
*G. rufescens,* Schilling (1913), p. 18.
*Glenodinium uberrimum,* Schilling (1913), p. 64.
*Gymnodinium rufescens,* West (1916), p. 53, fig. 38 A.

Diagnosis.—A small species with rotund body, its length 1.04 transdiameters; girdle displaced its own width; sulcus short on epicone, extending to antapex; yellow to brown chromatophores; red stigma; tendency to chain formation. Length, 45μ. Dublin, Ireland; Lake Geneva, Switzerland.

Description.—The body is rotund biconical to ellipsoidal with rounded apices, its length 1.04 transdiameters at the widest part. The epicone and hypocone are subequal and both are subconical to subhemispherical in shape. The epicone has a length on the left and right sides of about 0.54 and 0.63 respectively of the total length of the body in chain. The apex is broadly rounded and the antapex is usually broadly notched.

The girdle is equatorial to slightly postmedian, its distance from the apex not exceeding 0.54 at its proximal junction and at its distal junction with the sulcus about 0.63 of the total length of the body, with a displacement of not over its own width in chain, but generally with no displacement at all. The furrow is wide, about 0.07 transdiameters, and quite deeply impressed. The longitudinal flagellum arises slightly below the distal junction of the girdle and sulcus.

The nucleus is spherical or ellipsoidal and filled with coarse beaded chromatin strands. The cytoplasm contains numerous small spherules and elongated yellow chromatophores radially arranged in the peripheral layer of the cytoplasm. A small spherical pusule is found at the proximal junction of the girdle and sulcus. A spheroidal red stigma is found in the posterior end of the sulcus.

Dimensions.—Length, 40–51μ, rarely 25μ; transdiameter, 38–42μ.

Occurrence.—Originally reported by Allman (1854, 1855) in immense numbers from deeply discolored pond water in Phoenix Park, Dublin, Ireland. Later Penard (1891) found it in Lake Geneva, Switzerland. The references of Imhof (1892), Lemmermann (1900, 1902, 1910), Schilling (1913), and West (1916) are only citations.

Comparisons.—*Gymnodinium rufescens* is one of the small group of this genus, mostly fresh-water forms, having chromatophores and limited apparently to a holophytic type of nutrition. It is most closely related, morphologically, to *G. mirabile, G. palustre, G. carinatum,* and *G. aeruginosum.* It shows the typical yellow or yellow ochre color characteristic of this group, and is the stoutest, most nearly spherical member. It lacks the keel at the left of the sulcus in *G. carinatum* and the girdle of *G. mirabile.*

SYNONYMY.—Although very clearly described by Allman (1854, 1855) as *Peridinium uberrima*, this species seems to have been neglected by subsequent investigators and monographers, such as Lemmermann (1910) and Schilling (1913), apparently because of the lack of access to the journals containing the original description. Allman's account of cyst formation, or the appearance of a delicate spherical pellicle (no girdle noted), is probably the reason for Schilling's allocation of the species to Glenodinium. Saville-Kent (1880–82) established, on inadequate grounds, a new genus *Melodinium* with Allman's *Peridinium uberrima* as the sole species, and still continued Allman's original error of stating that the whole body was covered with cilia, an observation based either on a coating of bacteria or on the optical illusion arising from the vibratile action of the transverse flagellum in a rapidly moving individual.

Penard (1891) includes this species as variety *rufescens* of his *G. mirabile*. Lemmermann later advanced the variety to specific rank. Schilling (1913) in his useful monograph of the fresh-water dinoflagellates fails to recognize the similarity of Allman's and Penard's forms and apparently on the basis of Allman's observation of a pellicular cyst and of Saville-Kent's suggestion that the species may be a shell-less developmental condition of a thecate species, places Allman's *uberrimum* in *Glenodinium* among the "unsichere Peridineen." There seems to be no ground for this transfer, as such cyst formation is a normal feature of the life history of the naked dinoflagellates.

## **Gymnodinium varians** Maskell

Text figure X, 23

*Gymnodinium varians* Maskell (1887), p. 7, pl. 1, fig. 9*a-b*.
*G. varians,* Schewiakoff (1893), p. 162.
*G. varians,* Lemmermann (1900), p. 116; (1910), p. 565, figs. 19–20, pp. 618, 619, 621.
*G. varians,* Hutton (1904), p. 331.
*G. minimum,* Klebs (1912), pp. 396, 419, 439, fig. 7 A, B.

DIAGNOSIS.—A minute species with ovoidal body, its length 1.3 transdiameters; girdle median, without displacement; sulcus extending from girdle to antapex; color, green. Length, 17μ. Wellington district of New Zealand; Buitenzorg, Java.

DESCRIPTION.—The body is ovoidal with its widest transdiameter premedian, narrower posteriorly, its length 1.5 transdiameters at the widest part. The epicone and hypocone are subequal in length, but the epicone is slightly greater in volume. It has a length of 0.4 of the total body length and is hemispherical in shape. The hypocone is somewhat more slender with blunt antapex.

The girdle is subequatorial in position and forms a complete circle around the body. The sulcus extends from the girdle to the antapex in a straight line. The flagellar pores are not indicated in Klebs's (1912) figures, but the location of the flagella would suggest that the pores might be found, one slightly below the other, at the junction of the girdle and sulcus.

The nucleus is spherical and centrally located. Its diameter is about 0.5 transdiameter in length. The color is green. Chromatophores minute rod-shaped, radially located in the periphery.

DIMENSIONS.—Length, 8–17μ; transdiameter, 6–12μ; diameter of nucleus, 4μ.

OCCURRENCE.—Figured by Maskell (1887) from the Wellington district of New Zealand. The only other occurrence recorded is by Klebs (1912) as *G. minimum* from fresh water in the Botanical Gardens at Buitenzorg, Java.

SYNONYMY.—*Gymnodinium minimum,* described by Klebs (1912) from Buitenzorg, Java, is undoubtedly the same form described earlier by Maskell (1887) from New Zealand.

Until the complete life history of the Dinoflagellata has been worked out in a sufficiently large number of species to allow of generalizations for the whole group the exact allocation of many of the smallest forms described can be made only tentatively. It is probable that some of these minute species, like *G. minimum*, may prove to be only a stage in the development of some larger form. Its small size places it near the bottom of the list in this respect in *Gymnodinium*, if not, indeed, among all Dinoflagellata. Its rod-shaped green chromatophores ally it to *G. viride.*

## **Gymnodinium vestifici** Schütt

Text figure Y, 10

*Gymnodinium vestifici* Schütt (1895), pl. 25, fig. 85.
*G. vestifici,* Lemmermann (1899), p. 358.
*G. vestifici,* Lohmann (1908), pp. 252, 268, 368, table B; (1911), p. 31.
*G. vestifici,* Paulsen (1908), pp. 97, 98, fig. 134.
*G. vestifici,* Ostenfeld (1913), p. 338.

DIAGNOSIS.—A small species with fusiform body, its length 3.13 transdiameters; girdle anterior, displaced its own width; sulcus short on both epicone and hypocone; surface striate on hypocone. Length, 47μ. Atlantic or Mediterranean at Naples.

DESCRIPTION.—The body is fusiform, pointed at both ends, more tapering anteriorly, its length 3.13 transdiameters at its widest part. The hypocone exceeds the epicone in length by 0.55 its own length. The epicone is short, with a length on the left and right sides of 0.25 and 0.34 respectively of the total length of the body. It is asymmetrically rounded anteriorly with a pointed apex which is excentrically deflected dorsalward. The hypocone is slightly broader than and over twice the length of the epicone, and in ventral view is less pointed with blunt antapex.

The girdle is placed in the anterior third of the body, joining the sulcus proximally about 0.25 and distally 0.34 of the total length of the body from the apex. It traverses a descending left spiral course, displaced its own width. The furrow is wide, 0.28 transdiameter, and deeply impressed. The sulcus is very short, extending but a short distance on either side of the girdle in a narrow slightly sinuous line. The flagella and flagellar pores were not observed by Schütt (1895).

The nucleus is a small ellipsoidal body found in the region of the girdle. Its major and minor axes are about 0.46 and 0.36 transdiameter in length respectively. It is filled with coarse, chromatin granules. A few refractive rodlets are noted in the mid and anterior regions, and in the peripheral layer many minute spherules are present. The surface of the hypocone is striate, with longitudinal lines, but none are figured for the epicone.

DIMENSIONS.—Length, 47μ; transdiameter, 15μ; nucleus, 6μ by 5μ.

OCCURRENCE.—This species was figured by Schütt (1895) from the collections of the Plankton Expedition from the Atlantic or from the Mediterranean at Naples. It is also recorded by Lohmann (1908, 1911) from the Baltic Sea off Kiel, Germany, where he found it throughout the year, reaching its maximum in August. Ostenfeld (1913) observed it in the Cattegat.

COMPARISONS.—Among striate species included in the subgenus *Lineadinium* this species presents the maximum relative enlargement of the hypocone at the expense of the epicone. A tendency in this direction is detected in *G. aureum* sp. nov., *G. achromaticum* Lebour, *G. attenuatum* sp. nov., *G. gracile* Bergh, *G. abbreviatum* sp. nov., and *G. puniceum* sp. nov. (figs. Y, 3, 8, 12; figs. Z, 3, 7, 5). The limitation of striae to the hypocone is similar to that in *G. herbaceum* Kofoid (fig. Y, 17). The species is a very aberrant one, widely divergent from the others in the genus.

## **Gymnodinium violescens** sp. nov.

Plate 6, figure 69; text figure X, 11

DIAGNOSIS.—A small species with biconical body, its length 1.42 transdiameters; girdle submedian, displaced about 3 times its own width; sulcus extending from girdle to antapex; color, pansy violet. Length, 60μ. Pacific off La Jolla, California, July.

DESCRIPTION.—The body is asymmetrical, biconical, almost rhomboidal, with rounded apices, its length 1.42 transdiameters at the widest part. Its dorsoventral and transdiameter are equal in length. The epicone and hypocone are subequal in size. The epicone has the general shape of a cone of about 80°, with broad, blunt apex. The left side of the base of the epicone is considerably higher than the right, but the sides are equal in length, throwing the apex to the right of the midplane of the body. The sides are slightly concave posteriorly and convex anteriorly. The epicone has a length on the left and right sides of 0.43 and 0.58 respectively of the total length of the body. The hypocone has the shape of a cone of about 65°, the left side of which is about 0.02 longer than the right. Both sides have a greater convexity than those of the epicone. The ventral surface is deeply grooved by the broad sulcus.

The girdle is submedian, its proximal end meeting the sulcus at a distance from the apex of 0.43 and the distal end of 0.58 of the total length of the body. It forms a left-wound spiral, the first half of the course taking a transverse or slightly anterior direction, the second half turning posteriorly with its distal end displaced about 0.25 transdiameter. The furrow is wide, about 0.07 transdiameter, and deeply impressed. The anterior border is undercut by the furrow which curves gradually outward to the posterior border. The borders are outlined by lines of bright yellow green.

The sulcus begins at the proximal end of the girdle and extends posteriorly to the antapex. The trough is about equal to the girdle in width anteriorly. Beyond the junction with the distal end of the girdle it becomes broader and deeper, the left side being deflected so widely that it becomes lost near the lateral border of the body in ventral view. The right side is deflected to a less extent, reaching a point nearer the antapex before fading out. The anterior flagellar pore opens at the proximal end of the girdle, the posterior pore about two widths of the girdle behind the distal end.

The nucleus is a large, ellipsoidal body found near the central part of the cytoplasm. Its long axis lies in the short plane of the body. Its major and minor axes are about 0.66 and 0.39 transdiameters in length respectively.

The pusules were unusually large. The anterior one was spherical and thrown forward into the epicone so that its outlet came at its posterior end. This reverses the usual position of this organelle in the Gymnodiniidae. The posterior pusule was thrown to the right, the opening being at the left side. It, also, was unique in that it had a slight purplish tinge. This may have been due to the masses of that color around it. The cytoplasm is clear and very finely granular. It contained no other cell inclusions except numerous small spherules of a bright yellow-green color. The most striking feature of the whole organism is its colored pigment. The general tone of the protoplasm is pearl blue, shading to light glaucous blue at the girdle and near the periphery. Near the surface are numerous, small, rounded or disk-shaped bodies, pansy violet near the apex, shading to amaranth purple near the antapex. These pigment masses are somewhat more numerous in the hypocone than in the epicone. No striations or other surface markings could be detected.

DIMENSIONS.—Length, 60$\mu$; transdiameter, 42$\mu$; axes of nucleus, 28$\mu$ and 16$\mu$.

OCCURRENCE.—This species is represented by a single specimen taken July 26, 1917, with a No. 25 silk net, in a haul 2.5 miles off La Jolla, California, from 80 meters to the surface and in a surface temperature of 21°8 C.

COMPARISONS.—The color of this species finds its nearest counterpart in *G. puniceum*. Different shades of the general color are represented by *Pouchetia purpurata* and *P. purpurescens*. Like most of the species in this genus containing colored pigment, it belongs in the subgenus *Gymnodinium*. In its rather stout, biconical shape it is allied to the subgenus *Lineadinium* (fig. Y), which is mainly composed of biconical species. *G. violescens*, however, lacks surface striae. It is quite distinct in proportions and color from the other two biconical species, *G. filum* Lebour (fig. X, 20) and *G. fusus* Schütt (fig. X, 5) of the subgenus *Gymnodinium*.

## Gymnodinium viride Penard

Text figure X, 24

*Gymnodinium viride* Penard (1891), pp. 11, 15, 22, 23, 33, 55, pl. 4, figs. 11–24.
*G. viride*, Imhof (1892), p. 175.
*G. viride*, Lemmermann (1900), p. 116; (1902), p. 260; (1910), p. 613, fig. 26, p. 623.
*G. viride*, West (1909), p. 189; (1916), p. 52, fig. 38A.
*G. viride*, Klebs (1912), p. 440.
*G. viride*, Forti (1913), p. 32.
*G. viride*, Cunha (1913), p. 105.
*G. viride*, Schilling (1913), pp. 19, 64.
Not *Gymnodinium viride* Schütt (1895), pl. 26, fig. 88 (= *Gyrodinium foliaceum*).

DIAGNOSIS.—A small species with ellipsoidal body, flattened dorsoventrally, its length 1.3 transdiameters; girdle displaced its own width; sulcus extending from near the apex to near the antapex; green chromatophores. Length, 35$\mu$. Lake Geneva, Switzerland; Brazil.

DESCRIPTION.—The body is ellipsoidal, widest at the middle and flattened dorsoventrally, its length 1.3 transdiameters at the widest part. The dorsoventral diameter is about 0.7 of the transdiameter. The epicone and hypocone are subequal in size with a tendency towards enlargement of the hypocone. The epicone is broadly rounded at the apex with a length on the left and right sides of about 0.43 and 0.48 respectively of the total length of the body. The hypocone is slightly wider anteriorly than the corresponding part of the epicone. The antapex is broadly rounded or slightly truncate.

The girdle is submedian in position, its distance from the apex at the proximal and distal ends being 0.43 and 0.48 respectively of the total length of the body. It is displaced posteriorly slightly more than its own width. The furrow is narrow and deeply impressed with overhanging borders. The sulcus begins midway between the girdle and apex and extends posteriorly to the antapex as a narrow, somewhat obscure trough.

The nucleus is a spheroidal body located in the central part of the epicone. Its axis is about 0.33 transdiameter in length. Numerous green, rod-shaped chromatophores are radially arranged through the cytoplasm.

DIMENSIONS.—Length, 35μ; transdiameter, 25μ; diameter of nucleus, 8μ.

OCCURRENCE.—Figured by Penard (1891) from Lake Geneva, Switzerland. Its occurrence has also been recorded by Cunha (1913) from Brazil.

COMPARISONS.—This species and *G. carinatum, G. palustre, G. aeruginosum, G. uberrimum,* and *G. mirabile* form a group possessing the same general morphological characters, namely, fresh-water forms with numerous chromatophores of green or yellow ochre color, and differing but little in general size and proportions. Like Cunha's (1913) record of *G. fuscum,* his finding of a cool temperate water species which is common in Lake Geneva in the tropical waters of Brazil raises the question of the specific identity of his organism with *G. fuscum*. It is possible, however, that this, like a few other species of dinoflagellates, such as *Prorocentrum micans,* is truly cosmopolitan in its range.

It is very close to *G. aeruginosum* in size and proportions, but differs in having green instead of bluish green chromatophores and in their being rod-shaped in form instead of elliptical disks.

## **Gymnodinium vorticella** Stein

Text figure X, 29

*Peridinium vorticella* Stein (1878), pp. 73, 78.

*Gymnodinium vorticella* Stein (1878), p. 90; (1883), pl. 3, figs. 1–4.

*G. vorticella,* Eyferth (1879), p. 19.

*G. vorticella,* Klebs (1883), p. 356; (1912), pp. 391, 429.

*G. vorticella,* Pouchet (1883), p. 402.

*G. vorticella,* Bütschli (1885), pp. 986, 1017, pl. 51, fig. 7.

*G. vorticella,* Schilling (1891*a*), pp. 244, 276; (1891*b*), pp. 200, 205, 206; (1913), p. 20, fig. 19. Based on Stein's (1878) figure.

*G. vorticella,* Dangeard (1892).

*G. vorticella,* Entz (1896), p. 22; (1902), p. 124; (1907), p. 17; (1909), pp. 253, 254; (1910), pp. 162, 164.

*G. vorticella,* Ludwig (1898), p. 299.

*G. vorticella,* Mez (1898), p. 216.

*G. vorticella,* Schönichen and Kalberlah (1900), p. 231; (1909), p. 252.
*G. vorticella,* Lemmermann (1900), p. 116; (1902), p. 260; (1910), pp. 565, 625, fig. 23. After Stein (1878).
*G. vorticella,* Levander (1900), pp. 58, 64, 96; (1901), p. 6.
*G. vorticella,* Dogiel (1906), p. 32.
*G. vorticella,* Küster (1908), p. 352.
*G. vorticella,* Kleiber (1911), p. 14.
*G. vorticella,* Lauterborn (1913), p. 868.
*G. vorticella,* West (1916), p. 53.

DIAGNOSIS.—A minute species, with ovoidal body, its length 1.1 transdiameters; girdle displaced half its own width; sulcus short on both epicone and hypocone; colorless, holozoic. Length, 24μ. In fresh-water ponds and swamps in central Europe.

DESCRIPTION.—The body is broadly ovoidal, widest posteriorly, its length 1.1 transdiameters. The epicone greatly exceeds the hypocone in size, its length being greater by 0.36 of its own length. It is dome-shaped, with broad base and rounded apex. It has a length on the left and right sides of about 0.52 and 0.58 respectively of the total length of the body. The hypocone has a length on the left and right sides of 0.25 and 0.29 of the total length.

The girdle is postmedian in position, its junction with the sulcus occurring at about 0.50 of the total length of the body from the apex. The furrow is deeply impressed and about 0.14 transdiameters in width. The sulcus is a shallow furrow reaching to near the antapex.

The nucleus is a small spheroidal body in the center of the epicone, having a diameter of about 0.2 transdiameter of the body. Food masses are frequently found in the colorless cytoplasm with few or many minute spherules. A red stigma is found in the posterior part of the sulcus. Nutrition is holozoic.

DIMENSIONS.—Length, 23–24μ; transdiameter, 20–21μ; diameter of nucleus, 4.5μ.

OCCURRENCE.—Figured by Stein (1883) from fresh water in the environs of Prag. Entz (1896) notes its abundance in fresh water in Hungary.

COMPARISONS.—This small colorless species is very close to Danysz's *G. musei* (fig. X, 3), but appears to differ from it in proportions, being more ovoidal and lacking in the posterior sulcal notch, as well as having but a single eyespot instead of two.

### **Gymnodinium wilczeki** Pouchet

Text figure Z, 8

*Gymnodinium wilczeki* Pouchet (1894), pp. 170, 205, pl. 22, fig. 1.
*G. wilczeki,* Lemmermann (1901), p. 358.
*G. wilczeki,* Paulsen (1908), p. 108.

DIAGNOSIS.—A medium sized species with ovoidal, deeply constricted body, its length 1.33 transdiameters; girdle without displacement; sulcus extending from girdle to antapex; surface ridged; color, green. Length, 80μ. Arctic Ocean, July.

DESCRIPTION.—The body is stout, ovoidal, its longest diameter postequatorial in the upper hypocone, its length 1.33 transdiameters at the widest part. The epicone exceeds the hypocone by about 0.28 of its own length. It is slightly asymmetrical, subconical (85°) towards the apex and rounded posteriorly. Its length above the girdle is about 0.56 of the total length of the body. The hypocone has a length of about 0.4 of the total length. It is somewhat broader than the epicone, with rounded sides and deeply excavated at the antapex by the distal end of the sulcus.

The exact outlines of the girdle are not shown in Pouchet's (1894) figure which shows a deep constriction in the region of the girdle. It appears to be without displacement and is slightly postequatorial in position. The furrow is about 0.1 transdiameter in width, deeply impressed with rounded borders. The sulcus extends from the girdle to the antapex, where it forms a deep, wide excavation that gives a bilobed appearance to the posterior portion of the body. The position of the flagellar pores was not indicated.

No internal structures are shown by Pouchet except a few small spherules near the periphery. The surface is marked by projecting ridges, about 12 across the ventral face of the body. These seem to fade out near the apices. The color is green.

DIMENSIONS.—Length, 80$\mu$; transdiameter, 60$\mu$. Pouchet (1894) gives its dimensions as 80$\mu$ by 75$\mu$. The proportions of his figure, however, do not bear out this measurement of the transdiameter. We have taken the proportions of his figure rather than distort it to conform to the proportions given in his text.

OCCURRENCE.—This form was figured by Pouchet (1894) from the collections made by the "La Manche," from the Arctic Ocean near Spitzbergen, July 31, 1892, in a surface temperature of 2°6 C to 3°6 C. This is the only occurrence on record.

COMPARISONS.—This species is tentatively included in the subgenus *Pachydinium* because of the general resemblance of its striations to those of other species included therein, such as *G. puniceum* sp. nov. (fig. Z, 5). The nearest approach to the cingular constriction appears in *G. coeruleum* Dogiel (fig. Z, 4). This is one of the most northern species of *Gymnodinium* thus far known.

### **Gymnodinium zachariasi** Lemmermann

Text figure BB, 3

*Gymnodinium palustre,* Zacharias (1899), pp. 142–144, figs. 1–9.
*G. zachariasi,* Lemmermann (1900), p. 116; (1902), p. 260; (1903), pp. 139, 146, 149.
*G. palustre,* Wesenberg-Lund (1904), pp. 106, 107.
*G. palustre,* Dogiel (1906), p. 31.
*G. zachariasi,* West and West (1906), p. 92.
*G. zachariasi,* Entz (1910), pp. 157, 158, 162, figs. 1–12 (questionable).
*G. palustre,* Kolkwitz (1911), p. 346, pl. 6, fig. 2 (in part = *G. palustre* Sch.).
*G. palustre,* Klebs (1912), p. 429.
*G. zachariasi,* Schilling (1913), p. 16, fig. 12.
*G. palustre,* Fauré-Fremiet (1914), p. 41.
*G. zachariasi,* West (1916), p. 53.

DIAGNOSIS.—A small species with ovoidal body, its length 1.57 dorsoventral diameters; girdle without displacement (?); sulcus (?); yellowish brown; extrudes pseudopodia. Length, 44$\mu$. Fresh-water lakes near Plön, Germany; the Irish lakes; Budapest, Hungary.

Description.—The body is ovoidal, its greatest width posterior, and its length 1.57 dorsoventral diameters, at the widest part. The epicone is long, exceeding the hypocone by 0.35 of its own length. It is symmetrically bell-shaped with rounded apex. Its length is about 0.56 the total length of the body. The hypocone is subhemispherical in shape with a length of 0.3 the total length of the body.

The girdle is slightly posterior to the middle of the body, having a distance from the apex of about 0.56 of the total length of the body. Zacharias (1899) has figured only the right lateral view of the organism, hence the displacement of the girdle and the length and position of the sulcus cannot be determined. The furrow is about 0.1 dorsoventral diameter in width and is deeply impressed.

The most striking feature about this organism is its formation of pseudopodia. These are thrown out from the ventral side, usually in front of the girdle, but they may arise from the girdle or posterior to it, presumably from the sulcus. They may be straight, blunt extensions of protoplasm or they may be variously branched, and considerably longer than the body. No evidence is given, such as food inclusions in the body, to indicate that these have a function concerned with the nutrition of the body. The only cell inclusions noted by Zacharias (1899) are rod-shaped, yellow-brown chromatophores closely crowded together in longitudinal lines in the peripheral zone.

Dimensions.—Length, 44μ; dorsoventral diameter, 16μ; transdiameter, 32μ. It is difficult to reconcile the dimensions given by Zacharias (1899) in his text with the dimensions of his figures. The proportions used above are taken from his figures, while the actual dimensions quoted above are his own. His figure 1 might be interpreted as a dorsal view, but it has the same proportions as his figures 4 to 9, which are undoubtedly lateral views. Lemmermann (1910) has undoubtedly noted this discrepancy, as he states that the cross-section of the body is circular, 32μ broad. The width of his (Zacharias, 1899) figures cannot be more than 28μ as they are drawn. The diameter of the cyst ranges from 25μ to 100μ.

Occurrence.—Figured by Zacharias (1899) from plankton collected in Uklei Lake near Plön, Germany, in November. Its occurrence has also been recorded by Entz (1910) near Budapest, Hungary, and by West and West (1906) from Irish lakes.

Comparisons.—Described by Zacharias (1899) as *G. palustre* Sch. and changed to *G. zachariasi* by Lemmermann (1900). It differs from *G. palustre* mainly in its formation of pseudopodia. The importance placed on this phenomenon as an evidence of holozoic nutrition (West, 1916) would seem to be unduly stressed, since no evidence is offered on that point in *G. zachariasi*. On the other hand abundant evidence is offered herewith to show that holozoic nutrition is quite general throughout *Gymnodinium* as well as other genera, with no signs of the formation of pseudopodia.

CHAPTER XIII

# GYMNODINIIDAE: GYRODINIUM

## **GYRODINIUM** nom. gen. nov.

Text figures B, CC–EE

*Gymnodinium,* Schütt (1895) in part, pl. 21, figs. 65–69; pl. 22, figs. 70, 71; pl. 25, figs. 81, 83.
*Spirodinium* Schütt (1896), p. 5, fig. 6.
*Spirodinium,* Lemmermann (1899), pp. 359, 360; (1910), pp. 613, 626–628, figs. 20–22, 27.
*Spirodinium,* Paulsen (1908), pp. 101–103, figs. 139–141.
*Spirodinium,* Schilling (1913), pp. 21, 22, figs. 21, 22.

### Diagnosis

Gymnodiniidae with girdle a descending left spiral, displaced more than 0.2 of the total length of the body; sulcus longitudinal or with a torsion of less than 0.5 transdiameter in the intercingular area, extending from apex to antapex, rarely with antapical loop. The nucleus is usually near the center of the body, filled with distinct moniliform chromatin strands; perinuclear membrane is rarely present. Pusules usually present, opening anteriorly into the anterior flagellar pore or posteriorly into the posterior pore, or both may be present and connected by a canal. No nematocysts; suface striate or smooth; chromatophores rarely present; plasma colored; pigment granules sometimes present. Holozoic nutrition generally; encystment in thin-walled membrane frequent. Length, 23–155$\mu$. Marine and fresh water, eupelagic and littoral and from arctic, temperate, and tropical seas; 48 species known.

### Organology

*Gyrodinium* in its organization forms the connecting link between *Gymnodinium* and *Cochlodinium*, having, on the one hand, species which approach the *Gymnodinium* type of girdle arrangement, as *G. truncatum* sp. nov. (fig. CC, 5), and, on the other hand, forms like *G. ochraceum* (fig. DD, 17), with a marked torsion of the body approaching the *Cochlodinium* type of structure. In the relative proportions of epicone and hypocone it shows a range of variations similar to that found in *Gymnodinium*.

*Gyrodinium* differs from the genus *Gymnodinium* mainly in the arrangement of its girdle, the proximal and distal ends of which have here become displaced anteroposteriorly more than one-fifth of the total length of the body, and their displacement may be as great as one-half the total length. The girdle


Fig. CC. *Gyrodinium.* 1. *G. caudatum* sp. nov. 2. *G. culeus* sp nov. 3. *G. pusillium* (Schilling). After Schilling (1891, pl. 10, fig. 15). 4. *G. parvulum* (Schütt). After Schütt (1895, pl. 25, fig. 84). 5. *G. truncatum* sp. nov. 6. *G. ovoideum* sp nov. 7. *G. acutum* nom. sp. nov. After Schütt (1895, pl. 21, fig. 66). 8. *G. ovum* (Schütt). After Schütt (1895, pl. 25, fig. 83). 9. *G. melo* sp. nov. 10. *G. intortum* sp. nov. 11. *G. falcatum* nom. sp. nov. After Schütt (1895, pl. 25, fig. $81_1$). 12. *G. biconicum* sp. nov. 13. *G. spumantia* sp. nov. 14. *G. capsulatum* sp. nov. 15. *G. hyalinum* (Schilling). After Schilling (1891, pl. 10, fig. 14). 16. *G. flavescens* sp. nov. 17. *G. cuneatum* nom. sp. nov. After Pouchet (1885*a*, pl. 4, fig. 32). 18. *G. foliaceum* nom. sp. nov. After Schütt (1895, pl. 26, fig. $88_1$). 19. *G. dorsum* sp. nov. 20. *G. flavidum* sp. nov. 21. *G. crassum* (Pouchet). After Pouchet (1885*b*, pl. 26, fig. 2*a*). 22. *G. contortum* (Schütt). After Schütt (1895, pl. 21, fig. $67_1$). × 500.

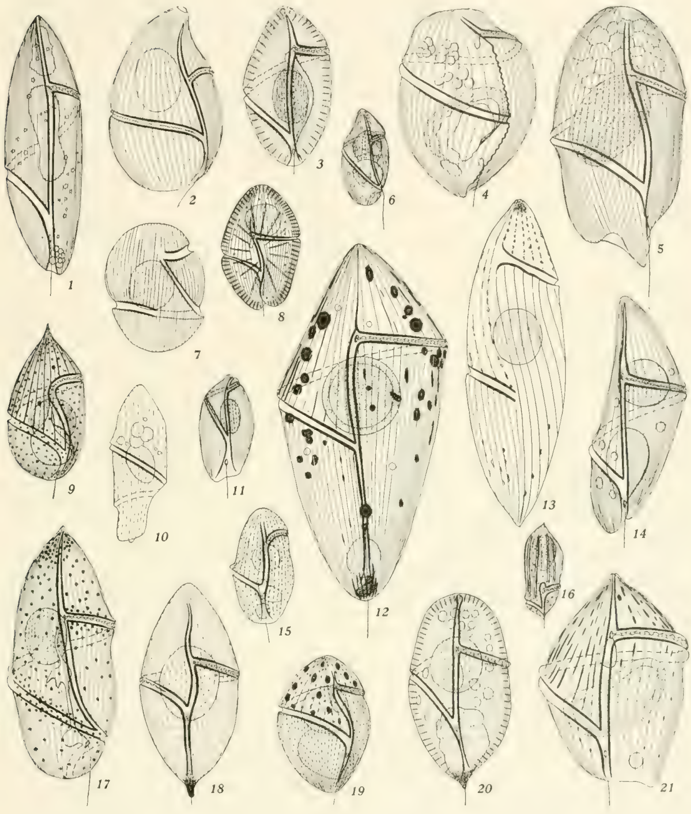


Fig. DD. *Gyrodinium.* 1. *G. submarinum* sp. nov. 2. *G. pepo* nom. sp. nov. After Schütt (1895, pl. 21, fig. 69). 3. *G. obtusum* nom. sp. nov. 4. *G. truncus* sp. nov. 5. *G. schuetti* (Schütt). After Schütt (1895, pl. 22, fig. $71_2$). 6. *G. herbaceum* sp. nov. 7. *G. grave* (Meunier). After Meunier (1910, pl. 14, fig. 27). 8. *G. fissum* (Levander). Original. 9. *G. fulvum* sp. nov. 10. *G. longum* (Lohmann). Modified after Lohmann (1908, pl. 17, fig. 22). 11. *G. viridescens* sp. nov. 12. *G. corallinum* sp. nov. 13. *G. britannia* nom. sp. nov. After Lebour (1917*b*, fig. 10*d*). 14. *G. spirale* (Bergh.). Original. 15. *G. pingue* (Schütt). Original. 16. *G. glaucum* (Lebour). Original. 17. *G. ochraceum* sp. nov. 18. *G. rubricaudatum* sp. nov. 19. *G. maculatum* sp. nov. 20. *G. postmaculatum* sp. nov. 21. *G. virgatum* sp. nov. × 500.

is thus here a more or less steeply descending left spiral, usually nearer the anterior than the posterior end, frequently occupying the middle third of the body. In one species only, *G. glaucum,* is it located far posteriorly. The amount of overlapping of the ends varies from none to about 0.5 transdiameter, the latter amount being rare and foreshadowing the conditions in *Cochlodinium* with its greater torsion of the body. The greatest amount of overlapping or overhanging is shown in *G. contortum* Schütt (fig. CC, 22).

The sulcus is variable in length, usually extending from or near the apex to the antapex in a nearly straight line or with a varying amount of torsion, less than 0.5 transdiameter. The sulcal region forms the area for the ingestion of food, which will probably account for the variations in length and prominence of its borders noted occasionally in individuals of the same species. In one species only, *G. ochraceum* (fig. DD, 17), it forms an antapical loop with a torsion of 0.5 transdiameter below the distal junction of the sulcus and girdle, resembling in this respect the more highly developed forms of *Cochlodinium* and *Pouchetia.* A greatly developed apical loop is found in *G. intortum* sp. nov. (fig. CC, 10), combined with an overhang of the girdle of 0.6 transdiameter which more closely aligns it with *Pouchetia* than with other members of this genus. Its lack of ocellus, however, excludes it from the genus *Pouchetia.*

The chromatin contents of the nucleus of *Gyrodinium* are always arranged in moniliform threads. In two species, *G. corallinum* sp. nov. and *G. virgatum* sp. nov. (figs. DD, 12, 21), the nucleus is composed of two distinct regions, an outer alveolar zone and an inner zone filled with chromatin granules, and separated by a distinct membrane. The nucleus is usually located near the central part of the body, rarely far anteriorly or posteriorly.

The surface of *Gyrodinium* may be either smooth or striate, with a preponderance of species showing a striate surface, differing in this respect from all other genera in the Gymnodiniidae. The striae may be continuous, unbroken lines or may be composed of linear series of short dashes. When pigment is present in the body it is collected along the lines of striae and massed at the ends of the lines, indicating a fundamental linear organization of the peripheral cytoplasm (figs. DD, 9, 21).

The color of the cytoplasm in *Gyrodinium* is remarkable for its diversity and brilliancy. It may be diffusely distributed as in *G. truncus* sp. nov. (pl. 3, fig. 28), *G. herbaceum* sp. nov. (pl. 10, fig. 109), and *G. fissum* sp. nov., confined to chromatophores, as in *G. melo* sp. nov. (pl. 5, fig. 50), *G. foliaceum* sp. nov., *G. falcatum* sp. nov., and *G. pusillum* (Schilling), or may take the form of pigment, as in *G. maculatum* sp. nov. (pl. 6, fig. 62), *G. corallinum* sp. nov. (pl. 10, fig. 117), *G. ochraceum* sp. nov. (pl. 7, fig. 76), *G. virgatum* sp. nov., *G. postmaculatum* sp. nov. (pl. 6, fig. 64).

All the colors of the spectrum are to be found within the species of this genus, but most of them show some shades of yellow and green. *G. maculatum* sp. nov. (pl. 6, fig. 62), with its violet pigment, is the only species lying near the violet end. *G. biconicum* sp. nov. (pl. 4, fig. 46) and *G. submarinum* sp. nov.

(pl. 10, fig. 110) are pale glaucous blue. A larger group is found at the red end, comprising *G. postmaculatum* sp. nov. (pl. 6, fig. 64), *G. corallinum* sp. nov. (pl. 10, fig. 117), *G. virgatum* sp. nov. (pl. 10, fig. 112), *G. britannia* nom. sp. nov., *G. cuneatum* sp. nov., *G. capsulatum* sp. nov. (pl. 5, fig. 54), *G. rubricaudatum* sp. nov. (pl. 10, fig. 116), and *G. culeus* sp. nov. (pl. 7, fig. 77), all exhibiting various tones of red and purple, in several cases in the form of pigment with a greenish yellow color in the cytoplasm, as in *G. corallinum* sp. nov. and *G. virgatum* sp. nov.

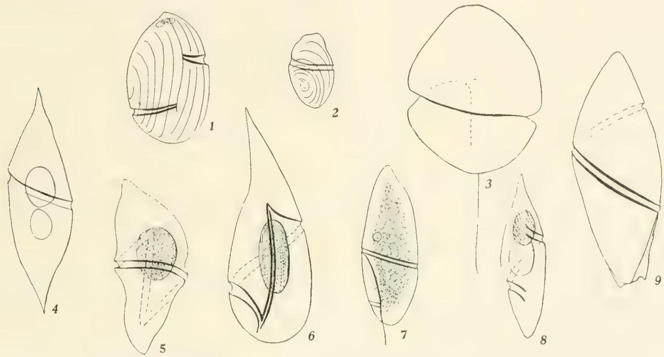


Fig. EE. *Gyrodinium.* 1 and 2. *G. concentricum* (Lebour). After Lebour (1917*b*, figs. 11*a*, *b*). 3. *G. fucorum* (Küster). After Küster (1908, fig. 1). 4. *G. fusiforme* nom. sp. nov. After Meunier (1910, pl. 14, fig. 25). 5. *G. mitra* (Schütt). After Schütt (1895, pl. 21, fig. 68$a_1$). 6. *G. lachryma* (Meunier). After Meunier (1910, pl. 14, fig. 21). 7. *G. ovatum* (Gourret). After Gourret (1883, pl. 1, fig. 22); magnification? 8. *G. fusiforme* nom. sp. nov. After Meunier (1910, pl. 14, fig. 23). 9. *G. cornutum* (Pouchet). After Pouchet (1885*a*, pl. 4, fig. 31). × 500.

Of the remaining thirty-seven species ten have been described without reference to their color and the others fall within the green-yellow part of the spectrum, varying from the mixed yellow green of *G. fissum* (Levander) (pl. 9, fig. 95) and *G. obtusum* nom. sp. nov. to the green of *G. herbaceum* sp. nov. (pl. 10, fig. 109), on the one hand, and on the other the yellow of *G. caudatum* sp. nov. to the deep yellow ochre of *G. ochraceum* sp. nov. (pl. 7, fig. 76). In the green and yellow group the latter color predominates, sixteen species exhibiting various shades of yellow and yellow ochre and seven exhibiting a green color with three of intermediate tones. One species only, *G. spumantia* sp. nov. (pl. 7, fig. 72), shows the presence of melanin.

*Gyrodinium* shows a distinct advance over the genus *Gymnodinium* in that the number of species possessing chromatophores has been reduced and the number of those possessing colored pigment has been increased. As in that genus, so also in *Gyrodinium* the latter group is composed of those species whose

color places them near the red end of the spectrum, a fact which links them with the further evolution of the Gymnodinioidae in the more highly specialized *Cochlodinium,* and in *Pouchetia,* and *Erythropsis.*

The species of this genus are, most of them, holozoic in nutrition. Four species only possess chromatophores, *G. melo* sp. nov., *G. falcatum* sp. nov., *G. pusillum* (Schilling), and *G. foliaceum* sp. nov. Of these *G. melo* and *G. foliaceum* show undoubted evidences of holozoic nutrition, such as the presence of food masses and vacuoles, products of metabolism, in the cytoplasm. The same conditon holds true in other Gymnodiniidae, as in *Amphidinium scissum, A. corpulentum, Gymnodinium agile, G. flavum,* and *G. herbaceum.* Of the remaining species most of them show evidences of holozoic nutrition, such as food balls, oil globules, vacuoles, and refractive granules in the cytoplasm, the accumulated products of metabolism or indications of periodic feeding and digestion.

Encystment is probably in many cases due to the ingestion of large food masses and follows upon it, the cyst being formed to meet the needs of the organism for a quiet period for its digestion. As the cyst wall is first formed it closely invests the body, becoming expanded at a later stage with the accumulation of fluid within it by osmosis. In many cases of encysted individuals, those enclosed in apparently newly formed cysts usually show the presence of food bodies as in *G. truncatum* (pl. 1, fig. 3), while others, in which the cyst has become greatly enlarged, may be entirely free from food bodies, as are individuals just emerging from the cyst.

## Distribution

*Gyrodinium,* like *Gymnodinium,* is widely distributed, but is found principally within the warm temperate waters. Two species only have thus far been described from fresh water, *G. hyalinum* (Schilling) and *G. pusillum* (Schilling) near Basel, Switzerland (Schilling, 1891); the former species is also recorded from the Danish lakes by Wesenberg-Lund (1904). Of the remaining twenty-three species three have been found within Arctic waters, *G. grave* (Meunier), and *G. lachryma* (Meunier) by Meunier (1910) near Nova Zembla, and *G. crassum* (Pouchet) by Pouchet (1894) near Spitzenbergen. One species, *G. spirale* (Bergh), has been recorded from the Indian Ocean by Karsten (1907). The remainder are inhabitants of the warm and cool temperate waters. The larger number of these come either from the Atlantic or the Bay of Naples, the localities from which Schütt's (1895) species were obtained. These are *G. acutum, G. contortum, G. foliaceum, G. obtusum, G. ovum, G. parvulum, G. pepo, G. pingue, G. mitra,* all figured and described by Schütt as in the genus *Gymnodinium,* and the following species described by Pouchet: in 1883, *G. fissum;* in 1885*a*, *G. crassum, G. cuneatum* (as *Gymnodinium gracile*), and in 1885*b*, *G. spirale,* all as in the genus *Gymnodinium.* From the Mediterranean at Cette Pavillard (1905) records *G. crassum* (Pouchet), Gourret (1883) from Marseilles

records *G. ovatum* (Gourret), and Schroder (1900) adds *G. obtusum* and *G. spirale* from Naples. The last named species is also recorded from the Baltic by Ostenfeld (1913), as is also *G. longum* (as *Cochlodinium longum* Lohmann) by Lohmann (1908) and *G. fissum* by Levander (1894*a*).

Lebour (1917*b*) has recorded the following from Plymouth Sound, England: *G. crassum, G. glaucum, G. britannia* (as *Spirodinium spirale* var. *acutum*), *G. spirale,* and one species, *G. concentricum,* which we place in the species *incertae sedis.* To these records Ostenfeld (1908) has added one of *G. fissum* from the Aral Sea with a question as to the identity of the species.

Thus far no record has been made of *Gyrodinium* in the Pacific. We record in this paper the occurrence in the plankton off San Diego and La Jolla, California, of the following species previously described: *G. contortum* (Schütt), *G. fissum* (Levander), *G. glaucum* (Lebour), *G. obtusum* (Schütt), *G. pingue* (Schütt), *G. sphaericum* Calkins, *G. spirale* (Bergh), and twenty-three new ones as follows: *G. biconicum, G. capsulatum, G. caudatum, G. corallinum, G. culeus, G. dorsum, G. flavescens, G. flavidum, G. fulvum, G. herbaceum, G. intortum, G. maculatum, G. melo, G. ochraceum, G. ovoideum, G. postmaculatum, G. rubricaudatum, G. spumantia, G. submarinum, G. truncatum, G. truncus, G. virgatum,* and *G. viridescens.*

Two species stand out in these records as cosmopolitan in distribution, *G. spirale* (Bergh) and *G. fissum* (Levander), the former occurring in the Atlantic, Pacific, and Indian oceans and the Mediterranean and Baltic seas, and the latter in the Atlantic and Pacific oceans and the Baltic Sea. The species having the widest range in temperate zones is *G. crassum* (Pouchet), recorded from the Mediterranean, the Atlantic, and the Arctic near Spitzbergen.

## Historical Discussion

In his "Peridiniales" in Engler and Prantl's *Pflanzenfamilien* Schütt (1896) established the genus *Spirodinium* for that section of the genus *Gymnodinium* in which the girdle forms a steep spiral and the sulcus or longitudinal furrow is a nearly straight line, with the result that the two flagellar pores are widely separated by the displacement of the distal end of the girdle posteriorly from the proximal. He named one species only, *S. spirale* (Bergh), as representing the genus. His name was later accepted by Lemmermann (1899, 1910), Paulsen (1908), Schilling (1913), and others working on the Dinoflagellata.

Unfortunately Schütt did not consider the possible preoccupation in zoological literature of his generic name, which may have been available from the botanical standpoint and was certainly appropriate and morphologically significant. However, many if not all of the species of this genus are holozoic, and in any event it is desirable to avoid preoccupation of generic names on both the plant and the animal side in the case of generic names among the flagellates.

In 1890 Fiorentini had used the generic name *Spirodinium* for a ciliate parasitic in the coecum of the horse, with *S. equi* as the monotype. It is there-

fore necessary, according to the zoological Code of Nomenclature, to displace Schütt's *Spirodinium* with a new generic name. We accordingly propose the appropriate and suggestive name *Gyrodinium* in lieu of *Spirodinium*. Its type species is *Gyrodinium spirale*, described as *Gymnodinium spirale* by Bergh (1881*b*) and used by Schütt (1896) as his type of the genus *Spirodinium*.

Schütt (1896), in thus calling attention to the need of revision of the genus *Gymnodinium*, failed to follow it up by removing from the genus those species which he had himself described earlier (1895) as species of *Gymnodinium*, but which possessed the characteristics of his new genus. Lemmermann later (1899) transferred some of these to *Spirodinium* as follows, which we cite with our own allocation:

*Gymnodinium cornutum* Schütt = *Spirodinium schuetti* (Schütt) Lemm. = *Gyrodinium schuetti* (Schütt) Kofoid and Swezy.

*G. spirale* var. *mitra* Schütt = *Spirodinium spirale* var. *mitra* (Schütt) Lemm. = *Gyrodinium mitra* (Schütt) Kofoid and Swezy.

*G. spirale* var. *obtusa* Schütt = *Spirodinium spirale* var. *obtusum* (Schütt) Lemm. = *Gyrodinium obtusum* (Schütt) Kofoid and Swezy.

*G. spirale* var. *pepo* Schütt = *Spirodinium spirale* var. *pepo* (Schütt) Lemm. = *Gyrodinium pepo* (Schütt) Kofoid and Swezy.

*G. spirale* var. *pinguis* Schütt = *Spirodinium spirale* var. *pingue* (Schütt) Lemm. = *Gyrodinium pingue* (Schütt) Kofoid and Swezy.

In addition to these species we have also transferred to *Gyrodinium* the following species described by Schütt (1895) as species of *Gymnodinium*:

*Gymnodinium contortum* Schütt = *Gyrodinium contortum* (Schütt) Kofoid and Swezy.

*G. opimum* Schütt = *Gyrodinium contortum* nom. sp. nov.

*G. ovum* (Schütt) = *Gyrodinium ovum* (Schütt) Kofoid and Swezy.

*G. parvulum* Schütt = *Gyrodinium parvulum* (Schütt) Kofoid and Swezy.

*G. viride* Schütt = *Gyrodinium foliaceum* nom. sp. nov.

*G. fusus* Schütt = *Gyrodinium falcatum* nom. sp. nov.

Lemmermann (1899 and 1900) also transferred to *Spirodinium* the following species described by the authors specified as species of *Gymnodinium*, which we cite here with our own allocation:

*Gymnodinium spirale* var. *nobilis* Pouchet = *Spirodinium spirale* var. *nobilis* (Pouchet) Lemm. = *Gyrodinium*, indeterminable.

*G. spirale* var. *cornutum* Pouchet = *Spirodinium cornutum* (Pouchet) Lemm. = *Gyrodinium cornutum* (Pouchet) Kofoid and Swezy.

*G. crassum* Pouchet = *Spirodinium crassum* (Pouchet) Lemm. = *Gyrodinium crassum* (Pouchet) Kofoid and Swezy.

*G. hyalinum* Schilling = *Spirodinium hyalinum* (Schilling) Lemm. = *Gyrodinium hyalinum* (Schilling) Kofoid and Swezy.

*G. pusillum* Schilling = *Spirodinium pusillum* (Schilling) Lemm. = *Gyrodinium pusillum* (Schilling) Kofoid and Swezy.

*G. fissum* Levander = *Spirodinium fissum* (Levander) Lemm. = *Gyrodinium fissum* (Levander) Kofoid and Swezy.

The number of species added later to the genus *Spirodinium* are few. In 1910 Meunier described *Spirodinium fusus*, overlooking the fact that the species name was preoccupied by Schütt's (1895) species. This we have designated

*Gyrodinium fusiforme* nom. sp. nov. He also described *Spirodinium lachryma* and *Spirodinium grave*, both of which we here transfer to *Gyrodinium*. Lebour (1917*b*) described *Spirodinium glaucum* and a doubtful species as *Spirodinium concentricum*, which we here transfer to *Gyrodinium;* also a form as *Spirodinium spirale* var. *acutum*, which is distinct from Schütt's species; this we have designated *Gyrodinium britannia* nom. sp. nov.

In addition to these we have transferred to *Gyrodinium* the following species originally allocated elsewhere but showing undoubted *Gyrodinium* characters:

*Gymnodinium ovatum* Gourret (1883) = *Gyrodinium ovatum* (Gourret) Kofoid and Swezy.

*Cochlodinium longum* Lohmann (1908) = *Gyrodinium longum* (Lohmann) Kofoid and Swezy.

Küster (1910) described a form, as *Gymnodinium fucorum*, which clearly belongs to this genus. His figures and description are inadequate for specific diagnosis, and we therefore place it among the species *incertae sedis*.

Twenty-one species have been previously described in other genera and are here included in *Gyrodinium*, as follows: *G. acutum* (Schütt), *G. contortum* (Schütt), *G. cornutum* (Pouchet), *G. crassum* (Pouchet), *G. fissum* (Levander), *G. foliaceum* (Schütt), *G. glaucum* (Lebour), *G. grave* (Meunier), *G. hyalinum* (Schilling), *G. longum* (Lohmann), *G. lachryma* (Meunier), *G. obtusum* (Schütt), *G. ovatum* (Gourret), *G. ovum* (Schütt), *G. mitra* (Schütt), *G. parvulum* (Schütt), *G. pepo* (Schütt), *G. pingue* (Schütt), *G. pusillum* (Schilling), *G. schuetti* (Schütt), *G. spirale* (Bergh).

We add to these in this paper the following twenty-three new species: *G. biconicum, G. capsulatum, G. caudatum, G. corallinum, G. culeus, G. dorsum, G. flavescens, G. flavidum, G. fulvum, G. intortum, G. herbaceum, G. maculatum, G. melo, G. ochraceum, G. ovoideum, G. postmaculatum, G. rubricaudatum, G. spumantia, G. submarinum, G. truncatum, G. truncus, G. virgatum, G. viridescens.*

The following species described under other names are for various reasons fully outlined in the discussion of the several species included in *Gyrodinium* under new names as follows: *Gyrodinium britannia* nom. sp. nov. (= *Gymnodinium spirale* var. *acutum*, Lebour, 1917*b*), *G. cuneatum* nom. sp. nov. (= *Gymnodinium gracile*, Pouchet, 1885*a*), *G. falcatum* nom. sp. nov. (= *Gymnodinium fusus*, Schütt, 1895, in part), and *G. fusiforme* nom. sp. nov. (= *Spirodinium fusus*, Meunier).

## Subgenera of **Gyrodinium**

Two subgenera based upon surface differentiations, as in *Gymnodinium*, may be separated in *Gyrodinium*. There are no species in this genus with the thick alveolar ectoplasm found in the species of the subgenus *Pachydinium* of *Gymnodinium*. The basis of separation of the two subgenera is the presence or absence of longitudinal striations in the ectoplasm. The more primitive subgenus *Laevigella* subgen. nov. lacks such markings. Its type species is *Gyrodinium caudatum* sp. nov. and it includes in addition twenty-four other species.

The more highly differentiated subgenus with striate pellicle has for its type species *Gyrodinium spirale* (Bergh), the type of *Gyrodinium sensu latu.* In addition to this it includes twenty-two other species. This subgenus contains the most of the species with maximum displacement of its girdle and torsion of the body, highest coloring, and development of pigment.

In addition there are imperfectly known species which must for the present be left unassigned in species *incertae sedis* to wit: *G. fucorum* (Kuster) and *G. concentricum* (Lebour).

### Subgenus 1. **Gyrodinium** (*sensu strictu*) subgen. nov., fig. DD

*Gyrodinium* with surface striate with parallel longitudinal striae. Type species is *G. spirale* (Bergh). This subgenus contains besides the type the following species: *G. britannia* nom. sp. nov., *G. corallinum* sp. nov., *G. crassum* (Pouchet), *G. cuneatum* nom. sp. nov., *G. fissum* (Levander), *G. fulvum.* sp. nov., *G. glaucum* (Lebour), *G. grave* (Meunier), *G. herbaceum* sp. nov., *G. longum* (Lohmann), *G. maculatum, G. obtusum* nom. sp. nov., *G. ochraceum* sp. nov., *G. pepo* (Schütt), *G. pingue* (Schütt), *G. postmaculatum* sp. nov., *G. rubricaudatum* sp. nov., *G. schuetti* (Schütt), *G. submarinum* sp. nov., *G. truncus* sp. nov., *G. virgatum* sp. nov., *G. viridescens* sp. nov.

### Subgenus 2. **Laevigella** subgen. nov., fig. CC

*Gyrodinium* with surface free from longitudinal parallel markings, with or without chromatophores. The type species is *G. caudatum* sp. nov. This subgenus includes besides the type the following species: *G. acutum* (Schütt), *G. biconicum* sp. nov., *G. capsulatum* sp. nov., *G. contortum* (Schütt), *G. cornutum* (Pouchet), *G. culcus* sp. nov., *G. dorsum* sp. nov., *G. falcatum* nom. sp. nov., *G. flavescens* sp. nov., *G. flavidum* sp. nov., *G. foliaceum* nom. sp. nov., *G. fusiforme* nom. sp. nov., *G. intortum* sp. nov., *G. hyalinum* (Schilling), *G. lachryma* (Meunier), *G. melo* sp. nov., *G. mitra* nom. sp. nov., *G. ovoideum* sp. nov., *G. ovatum* (Gourrett), *G. ovum* (Schütt), *G. parvulum* (Schütt), *G. pusillum* (Schilling), *G. spumantia* sp. nov., and *G. truncatum* sp. nov.

### Key to the Species of **Gyrodinium**

| | | |
|---|---|---|
| 1. Surface free from striae or other markings, with or without chromatophores | (subgenus **Gyrodinium**) | 7 |
| 1. Surface striate, chromatophores absent | (subgenus **Laevigella**) | 2 |
| 2. Chromatophores present | | 3 |
| 2. Chromatophores absent | | 6 |
| 3. Chromatophores yellow | | 4 |
| 3. Chromatophores green | | 5 |
| 4. Chromatophores small, rod-shaped, yellow ochre | **falcatum** nom. sp. nov. | |
| 4. Chromatophores disklike, yellow | **pusillum** (Schilling) | |

5. Body rotund ellipsoidal, girdle with distinct overhang, length over $60\mu$ ........**melo** sp. nov.
5. Body rotund, length less than $60\mu$ ........**foliaceum** nom. sp. nov.
6. Plasma colored ........ 7
6. Colorless, small fresh-water species ........**hyalinum** (Schilling)
7. Over $140\mu$ long ........ 8
7. Less than $140\mu$ long ........ 9
8. Body slender fusiform, peripheral zone of rodlets ........**acutum** (Schütt)
8. Body subovoidal, no peripheral rodlets, plasma vacuolated ........**spumantia** sp. nov.
9. More than $90\mu$ long ........ 10
9. Less than $90\mu$ long ........ 14
10. Sulcus with torsion of 0.5 transdiameter ........**contortum** (Schütt)
10. Sulcus without torsion ........ 11
11. Girdle displaced 0.5 length of body ........**lachryma** (Meunier)
11. Girdle displaced less than 0.5 length of body ........ 12
12. Body fusiform ........ 13
12. Body rotund ellipsoidal ........**flavidum** sp. nov.
13. Body with attenuate apices ........**fusiforme** nom. sp. nov.
13. Body with blunter apices, antapex with flaps or sulcus ........**cornutum** (Pouchet)
14. Sulcus with torsion ........ 15
14. Sulcus without torsion ........ 18
15. Torsion of sulcus, one turn ........**intortum** sp. nov.
15. Torsion less than one turn ........ 16
16. Length of body less than 2 transdiameters, color yellow ........**flavescens** sp. nov.
16. Length of body more than 2 transdiameters ........ 17
17. Length of body 3.5 transdiameters, epicone attenuate ........**biconium** sp. nov.
17. Length less than 3 transdiameters, epicone stouter ........**ovatum** (Gourret)
18. Small species, less than $35\mu$ in length ........ 19
18. Length more than $35\mu$ ........ 20
19. Body stout, length 1.4 transdiameters ........**ovum** (Schütt)
19. Body more slender, length 2.2 transdiameters ........**parvulum** (Schütt)
20. Rose colored granules present ........**culeus** sp. nov.
20. No rose colored granules ........ 21
21. Girdle displaced more than 1 transdiameter ........**mitra** nom. sp. nov.
21. Girdle displaced less than 1 transdiameter ........ 22
22. Apices prolonged in rounded horns ........**caudatum** sp. nov.
22. Apices not prolonged ........ 23
23. Body broadly biconical, antapex pointed ........**truncatum** sp. nov.
23. Body ellipsoidal, apices broadly rounded ........ 24
24. Length more than 1.5 transdiameters ........**dorsum** sp. nov.
24. Length less than 1.5 transdiameters ........ 25
25. Color primuline yellow, length $72\mu$ ........**ovoideum** sp. nov.
25. Color orange green ........**capsulatum** sp. nov.
27. Striae on epicone only, rose red pigment ........**cuneatum** nom. sp. nov.
27. Striae on both epicone and hypocone ........ 28

28. Large species more than $100\mu$ in length ........ 29
28. Not more than $100\mu$ in length ........ 35
29. Length more than 3 transdiameters ........ 30
29. Length less than 3 transdiameters ........ 31
30. Color bluish, girdle displaced 1.75 transdiameters ........ **submarinum** sp. nov.
30. Color yellowish with carmine pigment, displacement 1.45 transdiameters ........ **britannia** nom. sp. nov.
31. With coral red pigment ........ **corallinum** sp. nov.
31. No red pigment ........ 32
32. Length less than 2 transdiameters ........ **schuetti** (Lemm.)
32. Length more than 2 transdiameters ........ 33
33. With scattered ochraceous pigment granules ........ **ochraceum** sp. nov.
33. No ochraceous granules ........ 34
34. Length $165\mu$, epicone stout, girdle displaced 0.92 transdiameter ........ **crassum** (Pouchet)
34. Length $105–150\mu$, epicone more tapering, girdle displaced 1.2 transdiameter ........ **spirale** (Bergh)
35. Medium sized species, over $50\mu$ in length ........ 36
35. Small species, less than $50\mu$ in length ........ 46
36. With scattered coral red pigment ........ 37
36. No red pigment, sometimes purplish ........ 38
37. Pigment scattered along striae ........ **virgatum** sp. nov.
37. Pigment massed at antapex ........ **rubricaudatum** sp. nov.
38. Purplish or violet ........ 39
38. Color yellow, if present ........ 40
39. Color amaranth purple, sometimes massed at antapex ........ **postmaculatum** sp. nov.
39. Color violet purple, blotches on the epicone ........ **maculatum** sp. nov.
40. Girdle displaced 1 transdiameter or more ........ 41
40. Girdle displaced less than 1 transdiameter ........ 42
41. Minutely striate, length 1.75 transdiameters ........ **obtusum** nom. sp. nov.
41. Coarsely striate, length 2.7 transdiameters ........ **longum** (Lohmann)
42. Epicone not flattened ........ 43
42. Epicone flattened, truncate, body stout ........ **truncus** sp. nov.
43. Epicone contracted to acute or blunt point ........ 44
43. Epicone broadly rounded ........ 45
44. Epicone bluntly pointed, striae similar on epicone and hypocone ........ **pepo** (Schütt)
44. Epicone acute, striae unlike on epicone and hypocone ........ **fulvum** sp. nov.
45. Length 1.3 transdiameters ........ **grave** (Meunier)
45. Length 1.8 transdiameters ........ **fissum** (Levander)
46. Girdle postmedian ........ **glaucum** (Lebour)
46. Girdle not postmedian ........ 47
47. Proximal end of girdle far anterior ........ **viridescens** sp. nov.
47. Proximal end of girdle at least 0.25 total length from apex ........ 48
48. Girdle displaced 1 transdiameter, length $38\mu$ ........ **herbaceum** sp. nov.
48. Girdle displaced 0.75 transdiameter, length $51\mu$ ........ **pingue** (Schütt)

## **Gyrodinium acutum** (Schütt)

Text figure CC, 7

*Gymnodinium spirale* var. *acuta* Schütt (1895), pl. 21, fig. 66.
*Spirodinium spirale* var. *acutum*, Lemmermann (1899), p. 359.
*S. spirale* var. *acuta*, Schröder (1900), p. 13.
*S. spirale* var. *acuta*, Pavillard (1905), p. 47.
Not *Spirodinium spirale* var. *acutum*, Lebour (1917*b*) (= *Gyrodinium britannia* nom. sp. nov.).

Diagnosis.—A large species with slender, fusiform body, its length 3.32 transdiameters; girdle a descending left spiral with slight overhang and displacement of 0.93 transdiameter; sulcus extending from apex to within a short distance of the antapex. Atlantic (?) or Bay of Naples.

Description.—The body is slender fusiform, wider posteriorly, tapering to both apices, its length 3.32 transdiameters at the widest part, which is in the posterior third of the body. The hypocone exceeds the epicone in size, its length being greater by 0.12 of its own length and its transdiameter by 0.09. The epicone is elongate conical, about 32°, with a narrow, blunt apex. It has a length on the left and right sides of 0.32 and 0.60 respectively of the length of the body. The antapex is slightly wider than the apex and blunt.

The proximal end of the girdle joins the sulcus at a point distant from the apex 0.32 of the total length of the body. Its course around the body is that of a rather steeply descending left spiral, with the distal end joining the sulcus at a distance from the apex of 0.60 of the total length of the body. The furrow has a width of about 0.06 transdiameter and is deeply impressed with smooth borders. The sulcus begins at the apex and extends posteriorly in a slightly sinuous line to within a short distance of the antapex. The anterior flagellar pore is found at the junction of the girdle and sulcus, the posterior pore midway between the distal junction and the antapex.

The nucleus is an ellipsoidal body lying near the midregion of the cytoplasm. It is filled with coarse, moniliform chromatin strands which lie in the plane of its long axis, which is slightly oblique to the longitudinal axis of the body. Its major and minor axes are 0.76 and 0.41 transdiameters in length respectively.

A small sacklike or club-shaped pusule opens into the anterior flagellar pore. The cytoplasm is finely granular. A double-contoured periplast is shown in Schütt's figure (text fig. CC, 7), but no reference is made to it in text or description. A peripheral layer of "Randstäbschen" or slender rodlets occupies a large proportion of the interior of the body. These are arranged nearly perpendicular to the surface, and probably correspond to the small blue-green rodlets found in many of our own specimens, as in *G. obtusum* (text fig. DD, 3). In the anterior part of the body is a large, closely massed cluster of small spherules. No notes have been given by Schütt on the color of the organism. The surface is without striae.

Dimensions.—Length, 143μ; transdiameter, 43μ; axes of nucleus, 33μ and 19μ.

Occurrence.—Figured by Schütt (1895) from material secured by the Plankton Expedition, presumably from the Atlantic or from the Bay of Naples.

Synonymy.—This was originally figured by Schütt (1895) as *Gymnodinium spirale* var. *acuta* and later transferred by Lemmermann (1899) to the genus *Spirodinium* as *S. spirale* var. *acutum*.

Comparisons.—This species is much larger than *Gyrodinium spirale*, being 143μ in length as compared with 60μ to 100μ of the other species. It also differs

in proportions, being more attenuate conical and lacking the distal curvatures of apex and antapex and surface striae characteristic of *G. spirale*. It thus appears to be as distinct from *G. spirale* as many other species of the genus. It is closely related to Meunier's (1910) species found in Arctic waters, *G. fusiforme* nom. sp. nov. (*G. fusus* Meunier) (fig. EE, 8) and *G. lachryma* (fig. EE, 6). The proportions, however, are different, particularly so in the case of the latter species, with its broad, blunt posterior end and slender attenuate anterior end. The location of Schütt's species is entirely unknown and the temperature relations of these species cannot be compared.

## **Gyrodinium biconicum** sp. nov.

Plate 4, figure 46; text figure CC, 12

Diagnosis.—This is a small species with slender fusiform body, its length 3.57 transdiameters; girdle a descending left spiral, displaced 0.57 transdiameter; sulcus extending from apex to antapex, with torsion of 0.5 transdiameter; color, pale glaucous blue. Length, 68μ. Pacific off La Jolla, California, July.

Description.—The body is slender fusiform, tapering sharply anteriorly, less so posteriorly, its length 3.57 transdiameters at the widest part. The epicone exceeds the hypocone in length by 0.18 of its own length. It is slender conical, about 45°, with a slight sinistral flexure above the anterior pore region. It has a length on the left and right sides of about 0.35 and 0.77 respectively of the total length of the body. The hypocone is slightly broader than the epicone, its posterior end forming a cone of about 70°, rounding anteriorly. The entire body has a slightly sigmoid curve in its general outline with the concavity on the right face.

The proximal end of the girdle meets the sulcus at a distance from the apex of 0.35 of the total length of the body. It follows a descending left spiral course around the body and its distal end joins the sulcus at a distance from the apex of 0.77 of the total length of the body, being displaced about 1.57 transdiameters, and with an overhang of about 0.25 transdiameter. The furrow has a width of about 0.15 transdiameter, and is deeply impressed with smooth borders. The sulcus is a narrow, shallow trough extending from the apex to near the antapex in a sigmoid curve which gives it a torsion of about 0.5 transdiameter. It terminates near the left side of the antapex. The anterior flagellar pore opens at the anterior junction of the sulcus and girdle and the posterior pore slightly below the posterior junction. The transverse flagellum traverses nearly the entire length of the girdle and the longitudinal flagellum has a length about equal to that of the body.

The nucleus is a spheroidal body located near the center of the organism. In the individual figured it was elongate ellipsoidal, evidently a predivision stage. Its axis in the other specimens was about 0.57 to 0.73 transdiameter in length.

A large globular pusule opens into the anterior flagellar pore, a smaller sacklike one into the posterior pore. The cytoplasm is very clear and transparent with few food bodies. In the apical region of both individuals an irregular, light yellow, refractive body was located. In the peripheral zone are numerous minute, blue-green oil droplets. The general color of the organism is a diffused pale glaucous blue. No striations or other surface markings were present.

Dimensions.—Length, 52–68μ; transdiameter, 15–19μ; axes of nucleus, 13μ and 11μ.

OCCURRENCE.—The first individual was taken July 13, 1917, with a No. 25 silk net, in a haul 1.25 miles off La Jolla, California, from 50 meters to the surface and in a surface temperature of 20°6 C. It was again observed in a haul made July 23, 6 miles off La Jolla, from 80 meters to the surface and in a surface temperature of 20°8 C.

COMPARISONS.—This species in its lack of striae on the surface and arrangement of girdle stands close to *G. mitra* (fig. EE, 5) and *G. fusiforme* (fig. EE, 8). It differs from them, however, in its proportions, overhang of girdle and torsion of the body. In the latter respect it recalls *G. spirale* (fig. DD, 14), without having the surface striae of that species. It is the only species in the genus with its general color blue, the dull glaucous blue of *G. submarinum* appearing almost green. It does not, however, approach the clear cornflower blue of *Gymnodinium coeruleum*.

## **Gyrodinium britannia** nom. sp. nov.

Text figure DD, 13

*Spirodinium spirale* var. *acutum*, Lebour (1917*b*), p. 194, fig. 10*d*.

DIAGNOSIS.—A large species with long, fusiform body, its length 3.29 transdiameters; girdle a descending left spiral displaced 1.42 transdiameters; sulcus extending from apex to antapex (?); surface sparsely striate; carmine-colored pigment. Length, 145μ. Plymouth Sound, England, August.

DESCRIPTION.—The body is long, slender fusiform, widest in the middle and tapering at both apices, its length 3.29 transdiameters at the widest part. The hypocone exceeds the epicone in length by about 0.26 of its own length. The epicone is subconical, about 50°, with slightly convex sides and blunt, subsymmetrical apex. It has a length on the left and right sides of the sulcus of 0.17 and 0.59 respectively of the total length of the body. The hypocone is more slender posteriorly than the epicone with a more pointed antapex. It is elongate conical posteriorly, about 45°, with a length on the left and right sides of 0.79 and 0.38 respectively of the total length of the body.

The girdle joins the sulcus at a distance from the apex of 0.17 of the total length of the body. It sweeps around the body in a descending left spiral course, displaced posteriorly 1.42 transdiameters. The furrow is wide, about 0.09 transdiameter, and deeply impressed. The sulcus is not definitely marked off as such in Lebour's (1917*b*) figure, but evidently extends from near the apex to or near the antapex. The flagella and pores are also omitted from her figure.

The nucleus is ellipsoidal and located near the central part of the body. It is filled with short, moniliform chromatin strands, which are parallel to the longitudinal plane of the body. Its major and minor axes are 0.59 and 0.5 transdiameters in length respectively. The surface of the body is covered with equidistant, longitudinal lines, figured as about 15 across the ventral face. These lines are further marked off by granules of carmine-colored matter, strung along their length like beads on a string. These are most numerous on the epicone, especially near the apex, with a few scattering granules on the posterior half of the hypocone.

DIMENSIONS.—Length, 145μ; transdiameter, 44μ; axes of nucleus, 25μ and 21μ.

OCCURRENCE.—Figured by Lebour (1917*b*) from Plymouth Sound, England, in August.

SYNONYMY.—This form was described by Lebour (1917*b*) as *Spirodinium spirale* var. *acutum* Schütt. It differs from Schütt's figure (1895), however, in its proportions and more strikingly in its coloring, and also in its cytoplasmic structure. Surface striae are apparently lacking in Schütt's species. These differences seem to be too great to allow it to remain with *Gyrodinium acutum*, hence we propose for it specific rank with the name *G. britannia*.

COMPARISONS.—In the possession of red pigment this species stands near *G. corallinum* (pl. 10, fig. 117) and *G. virgatum* (pl. 10, fig. 112), differing from them, however, in other important respects, such as proportions and shape of body and type of nucleus (see figs. DD, 12, 13, 21).

### **Gyrodinium capsulatum** sp. nov.

Plate 5, figure 54; text figure CC, 14

DIAGNOSIS.—This is a small species with broadly ovoidal body, its length 1.26 transdiameters; girdle submedian, a descending left spiral displaced 0.38 transdiameter; sulcus short on epicone, extending to antapex; color, orange green. Length, 45μ. Pacific off La Jolla, California, July, August.

DESCRIPTION.—The body is broadly ovoidal, with broad, rounded apices, widest posteriorly, its length 1.26 transdiameters at the widest part. The epicone exceeds the hypocone in length by about 0.2 of the total length, but not in volume, as its transdiameter is narrower. The epicone is smoothly rounded with broad apex. It has a length on the left and right sides of 0.4 and 0.69 respectively of the total length of the body. The hypocone is hemispherical in shape, somewhat wider than the epicone, with smoothly rounded or slightly notched antapex.

The girdle is submedian in position, its proximal end joining the sulcus at a distance from the apex of 0.4 and its distal end 0.69 of the total length of the body. It follows a descending left spiral course around the body, its distal end displaced about 0.38 transdiameter. The furrow is wide, about 0.08 transdiameter in width, and is deeply impressed with smooth, overhanging borders. The sulcus invades the epicone for a short distance, narrowing rapidly from a wide trough at the girdle to a slender line. Posterior to the anterior flagellar pore the overhanging borders of the sulcus nearly obliterate the furrow, immediately spreading out again to form a wide, deep trough which reaches to the antapex. Its borders are mobile, overhanging, giving a slightly sinuous line to the course of the sulcus. The anterior flagellar pore is found about 0.5 of the width of the girdle posterior to the proximal junction of the girdle and sulcus, and the posterior pore is slightly behind their distal junction.

The nucleus is a large, ellipsoidal body situated immediately below the equatorial plane, with its major axis slightly oblique to the short axis of the body. It is filled with fine, moniliform chromatin strands following the course of its major axis. Its major and minor axes are about 0.73 and 0.44 transdiameter in length respectively.

In the individual figured pusules were not evident. In another specimen a single long, tube-like pusule opened into both the anterior and posterior pores. The cytoplasm is finely granular and transparent. Scattered through it are greenish yellow patches of irregular shape and a few oil droplets of the same color. Near the periphery are numerous club-shaped vacuoles filled with the pink fluid such as is found in the pusules. These appear to be in the process of opening to the exterior. The color is pale green yellow distributed throughout the cytoplasm. Beneath the pellicle is a layer of orange color which forms a border around the body in optical section. A clearly marked, double-contoured periplast forms the periphery of the body. Around the body and closely following its contour is a hyaline thin-walled cyst. A second cyst is formed around this, much larger than the first and closely following its outline.

DIMENSIONS.—Length, 45–50$\mu$; transdiameter, 33–40$\mu$; major and minor axes of nucleus, 25$\mu$ and 28$\mu$; length of outer cyst, 62$\mu$.

OCCURRENCE.—The individual figured was taken July 2, 1917, 6 miles off La Jolla, California, with a No. 25 silk net, in a haul from 60 meters to the surface and in a surface temperature of 21.9 C. It was noted again on August 6, in a surface haul 4 miles offshore and in a surface temperature of 21°2 C.

COMPARISONS.—This species stands nearest to *Gymnodinium* in its type of girdle arrangement, having somewhat less displacement than other species of the genus. The orange color in its peripheral layer recalls the same color and location in *Gymnodinium dogieli* (pl. 3, fig. 34) and *G. pachydermatum* (pl. 3, fig. 32), without, however, being correlated with the characteristic ectoplasmic differentiation of those species.

## **Gyrodinium caudatum** sp. nov.

Plate 9, figure 102; text figure CC, 1

DIAGNOSIS.—Body broadly fusiform, its length 1.94 transdiameters, with apical and antapical processes subequal, very stout, the apical truncate; girdle displaced about 0.5 transdiameter, with slight overhang; color, primuline yellow; length, 66$\mu$. Pacific off La Jolla, California, July.

DESCRIPTION.—The body is broadly fusiform with abruptly contracted apical and antapical processes, its length 1.94 transdiameters; dorsoventral and transdiameters equal. Epicone and hypocone are about equal. The epicone has a length on the left and right sides of 0.27 and 0.59 transdiameters respectively. It is subhemispherical above the proximal end of the girdle and contracts to a stout apical process in the form of a truncate cone 0.27 transdiameter in length, its basal diameter equaling its altitude, and stout, slightly truncate apex having a diameter of 0.66 of its base. It is slightly deflected dorsally. The hypocone is similar in size and general form to the epicone, tapers a trifle more gradually into the antapical process, which in our specimen is conical, with a length of approximately 0.4 transdiameter and a basal diameter of 0.66 its length. It is deflected ventrally for about 10° from the axis. The antapex is broadly rounded.

The girdle forms a descending left spiral displaced distally about 0.25 the total length of the body, with slight overhang. The furrow is rounded, deeply impressed in its proximal part, less so distally, and has no protuberant or overhanging lips. The anterior flagellar pore is at the upper angle of the proximal end, and the flagellum traverses about 0.5 of the circumference. The sulcus could be traced for a short distance as a narrowing groove anterior to the girdle. It passes posteriorly with a sigmoid flexure to about an equal distance beyond its junction with the distal end of the girdle. The posterior flagellar pore lies midway between the two ends of the girdle.

No surface markings could be found on the pellicle. The nucleus lies near the center of the midbody to the right and below the proximal end of the girdle. It contains numerous beaded chromatin threads polarized to the left and anteriorly. It seems to be crowded to one side by the large, opaque, dull greenish yellow mass enclosed in a vacuole, probably a food ball. Adjacent to this are several highly refractive oil globules. A small sacklike pusule with pinkish contents forms a diverticulum directed posteriorly from the anterior flagellar pore. A sulphine-yellow sphere is found in the posterior part of the hypocone.

The whole body is suffused with a primuline yellow tint fading in the antapical process to a light chalcedony yellow.

The body is enclosed in a very thin and exceedingly transparent cyst wall which is closely applied to the body, even sinking into the furrow of the girdle. About the apical and antapical processes it is distended and is prolonged beyond each in finger-like processes of equal length, about 0.66 that of the body. This distension indicates a difference in the osmotic properties or capacities of the membrane in these regions or a localized permeability of the body permitting greater exudation in these terminal surfaces.

DIMENSIONS.—Length, of body 66µ, of total cyst 137µ; transdiameter, 33µ.

OCCURRENCE.—Described from a single individual taken in a haul of a No. 25 silk net from 80 meters, 4 miles offshore at La Jolla, California, in the California Current in surface temperature of 19°8 C on July 9, 1917. It was again found July 23, in a haul 6 miles offshore in 80 meters to the surface and a surface temperature of 20°8 C.

COMPARISONS.—This species bears a superficial resemblance to *Gymnodinium fusus* Schütt (1895, pl. 24, fig. 79, pl. 25, fig. 81), yet differs from both the forms which Schütt has figured under this name, the first of which is a *Gymnodinium*, the second we have placed in *Gyrodinium* as *G. falcatum* nom. sp. nov. Our species resembles *G. falcatum* (fig. CC, 11) in the presence of distinct apical processes which are distinct from the midbody and blunt at the ends, features which distinguish these two species from all other fusiform species of the genus. There is a possibility that there might be some change in form incident upon release from the cyst, yet such changes have not occurred in our material except in one individual in which the body was filled with large food masses. This was enlarged posteriorly but without change anteriorly. Schütt's form shows many yellow-ochre chromatophores which are totally lacking in our species. It was also larger, measuring 122µ as compared with 66µ, the length of our form.

## Gyrodinium concentricum (Lebour)

Text figures EE, 1, 2

*Spirodinium concentricum* Lebour (1917*b*), p. 194, fig. 11.

Under this name Miss Lebour has figured a *Gyrodinium* characterized by concentric lines arranged around a certain point on the side or dorsal surface of the body. The body is colorless with a shape and girdle arrangement like *G. obtusum* Schütt. This is evidently a species of *Gyrodinium* parasitized by a species of *Amoebophrya* Köppen. Forms parasitized by some member of this genus have been observed in our own material and present the coiled appearance shown in Lebour's figure. This explanation seems to be borne out by her own statements of the inconstancy in position of the spiral, the variations in size of the organism and that it was of rare occurrence. Sufficient data are not given to identify the *Gyrodinium*; we, therefore, place it among the species of doubtful status as undeterminable.

## **Gyrodinium contortum** (Schütt)

Text figure CC, 22

*Gymnodinium contortum* Schütt (1895), p. 11, pl. 21, fig. $67_{1-3}$.
*Gymnodinium opimum* Schütt (1895), pl. 21, 68*b*.
*Spirodinium opimum*, Lemmermann (1899), p. 360.

Diagnosis.—A large species with ovoidal body, its length 2.68 transdiameters at the widest part; girdle a descending left spiral, displaced 1.4 transdiameters; sulcus extending from near the apex to the antapex; surface striate; color, yellow ochre. Length, 134μ. Atlantic or Bay of Naples.

Description.—The body is long ovoidal, tapering anteriorly and rounded posteriorly where it is widest in its posterior third, its length 2.68 transdiameters at the widest part. The epicone exceeds the hypocone in length by 0.1 of its own length, but, owing to its narrower width, is not greater in size. It is conical in shape (40°) with blunt apex. It has a length on the left and right sides of 0.24 and 0.77 of the total length of the body. The hypocone is broader than the epicone with a rounded antapex which is notched on the ventral face by the distal end of the sulcus.

The girdle joins the sulcus at a distance from the apex of 0.24 of the total length of the body. It turns posteriorly at an angle of 35° from the horizontal plane in its spiral course around the body, decreasing the steepness of its course in the last quarter of its length, meeting the girdle distally at an angle of about 20° from the horizontal. It is displaced 1.4 transdiameters at the widest part of the body. The furrow is wide, 0.08 transdiameter in width, and deeply impressed. The sulcus begins below the apex and passes posteriorly with a strong left deflection, giving it a torsion of about 0.5 transdiameter. It is enlarged near the antapex to about twice its width anteriorly.

The nucleus is ellipsoidal and midventrally placed. Its chromatin contents are arranged in coarse strands following its long axis. Its major and minor axes are 0.74 and 0.42 transdiameters in length respectively. Numerous vacuoles of varying sizes are scattered through the cytoplasm. In the peripheral zone is a layer of rodlets, radially arranged. The surface is striate with equidistant, longitudinal striae.

Dimensions.—Length, 111μ to 134μ; transdiameter, 45μ to 50μ; axes of nucleus, 37μ and 21μ.

Occurrence.—Figured by Schütt (1895) from the collections of the Plankton Expedition from the Atlantic or from the Bay of Naples. A single individual was taken July 19, 1906, 1.5 miles off La Jolla, in a surface haul with a No. 20 net. This individual was dark yellow ochre in color.

Synonymy.—Schütt (1895) figured as two distinct species two forms, *Gymnodinium contortum* and *G. opimum*, which we have here placed as synonymous. Their size differs slightly, *contortum* having a length of 134μ and a width of 50μ and *opimum* 111μ and 45μ, a difference within ordinary species variation. Both are ovoidal in outline, widest posteriorly (Schütt's fig. 68*b*, pl. 21 (1895) of *G. opimum* is evidently oriented wrong end uppermost), with the same or nearly the same relative proportions and surface striae as in his *G. contortum*.

Comparisons.—*Gyrodinium contortum*, in its wide displacement of the girdle and its overhang, resulting from the torsion of the sulcus, leads onward in the line of evolution to the next genus, *Cochlodinium*. The torsion of the intercingular part of the sulcus in this species is greater than in *G. ochraceum* sp. nov. (fig. DD, 17), though without the antapical loop of that species, which gives its entire sulcus a slightly greater torsion than in *G. contortum*. It belongs in this group of ochraceous striate species, including *G. ochraceum* sp. nov. and *G. fulvum* sp. nov. (figs. DD, 9, 17), all of which appear to lack chromatophores. It is clearly distinguishable from these by its proportions.

## Gyrodinium corallinum sp. nov.

Plate 10, figure 117; text figure DD, 12

Diagnosis.—A large species with asymmetrically biconical body, its length 1.96 transdiameters; girdle a premedian, descending left spiral, displaced 0.62 transdiameter; sulcus extends from girdle or near apex to antapex; surface moderately striate; color, greenish yellow with scattered coral-red pigment. Length, 155μ. Pacific off La Jolla, California, July.

Description.—The body is asymmetrically biconical, nearly subrhomboidal in shape, its longest transdiameter slightly premedian, its length 1.96 transdiameters at the widest part. A cross-section of the body is nearly circular. The hypocone far exceeds the epicone in size, its length being greater by 0.21 of its own length. The epicone has the shape of a broad cone of about 70° with blunt apex. It has a length on the left and right sides of 0.26 and 0.59 respectively of the total length of the body. The sides of the epicone are nearly straight or sometimes slightly concave on the right side. The hypocone is elongate conical, of about 40°, with sides somewhat more convex than those of the epicone. It has a length on the left and right sides of the body of 0.72 and 0.42 respectively of the total length of the body. The blunt antapex is slightly wider and more rotund than the apex.

The girdle is premedian in position for the greater part of its length. Its proximal end joins the sulcus at a distance from the apex of 0.26 of the total length of the body. It follows a descending left spiral course around the body, the first 0.5 transdiameter of which is nearly in a transverse direction, gradually steepening onward until it joins the sulcus at a distance from the apex of 0.59 of the total length of the body, and at an angle of about 55° with the longitudinal plane of the body. Its distal end is displaced posteriorly about 0.62 transdiameter. The furrow has a width of about 0.06 transdiameter, and is deeply impressed with smooth borders. The sulcus begins near the apex and extends posteriorly in an almost straight line to the antapex. On the epicone it is narrow almost to invisibility in some individuals. In others, particularly those having food masses present, it is wider, showing the evident correlation of the sulcal area and food ingestion. The anterior flagellar pore is found at the anterior junction of the girdle and sulcus, the posterior pore midway between the posterior junction and the antapex.

The nucleus is large, spherical and slightly premedian in position. It is differentiated into two distinct parts. The outer, circular zone, which is about 0.1 of the total transdiameter of the nucleus in width, is composed of pinkish vacuoles, elongated in optical section with the long axis at right angles to the surface of the nucleus. Outside of these is a clear, double-contoured membrane. The inner zone is apparently separated from the alveolar layer by a membrane or a very thin, clear area. The central area is completely filled with chromatin granules without evident linear arrangement. The axis of the nucleus is about 0.47 transdiameter in length.

Small sacklike pusules open into each flagellar pore. The cytoplasm is clear and transparent and greenish yellow in color. Small, green oil droplets, a few dark refractive granules, and a number of large pink vacuoles were scattered through it. The surface is striate. On the epicone the striae are about 20 in number across one face, and on the hypocone about 1.5 times as many. The striae are blue green in color. Scattered along the line of striae are masses of coral-red fluid pigment. On the epicone these are elongated, sometimes extending from the girdle to near the apex in an unbroken line or they may be in shorter, thicker masses. On the hypocone they are fewer in number, and more variable in size, usually minute and scattered scantily along the striae, like beads on a string. Just underneath the pellicle are a number of large rounded masses of pigment. These are found in both epicone and hypocone, but are more numerous and larger in size in the epicone. Several of the elongated rodlike masses are found at the antapex. Some individuals observed contained large bodies and many vacuoles, evidences of holozoic nutrition in this species.

Dimensions.—Length, 124–158μ; transdiameter, 52–80μ; transdiameter of nucleus, 30–40μ.

Occurrence.—Two specimens were taken July 9, 1917, with a No. 25 silk net, 4 miles off La Jolla, California, in a haul from 80 meters to the surface and in a surface temperature of 19°2 C. It was found again on July 11, in approximately the same place and with the same apparatus.

Comparisons.—In its nuclear structure, color, and arrangement of pigment this species closely resembles *G. virgatum* (pl. 10, fig. 112; fig. DD, 21). In the relative proportions of the body and girdle displacement, however, it shows considerable differences. The posterior portion of *G. virgatum* is somewhat distorted by the recent ejection of a food body, but this could hardly account for the differences in size and proportion. The hypocone of *G. corallinum* is more finely striate, its displacement of girdle in relation to the transdiameter less, and its posterior flagellar pore much farther below the posterior junction of girdle and sulcus than in *G. virgatum*.

## **Gyrodinium cornutum** (Pouchet)

Text figure EE, 9

*Gymnodinium spirale* var. *cornutum* Pouchet (1885*a*), p. 69, pl. 4, fig. 31.
*Spirodinium cornutum,* Lemmermann (1899), p. 359.
Not *Gymnodinium cornutum* Schütt (1895), pl. 22, fig. 71 (= *Gyrodinium schuetti* (Schütt)).

Diagnosis.—A medium sized species with spindle-shaped body, its length 2.8 transdiameters; girdle a descending left spiral, displaced about 1.21 transdiameters; sulcus apparently extending to the antapex; color, greenish. Length, 104μ. Atlantic off Concarneau, France, June.

Description.—The body is spindle-shaped, widest at the middle and tapering towards both ends, its length 2.8 transdiameters at the widest part. The epicone is exceeded in size by the hypocone, its length being 0.11 of its length less than that of the hypocone. The epicone is conical (55°) with a narrow, blunt apex. Its length on the left and right sides is 0.24 and 0.67 of the total length of the body. The hypocone has a blunt antapex and is further marked off by two protuberances on the ventral face which are probably the borders of the sulcal region.

The girdle begins at a distance from the apex of 0.24 of the total length of the body. It passes around the body in a steep descending left spiral course, becoming displaced 0.67 transdiameters. The furrow has a width of about 0.08 transdiameter and is deeply impressed. The sulcus is not figured by Pouchet (1885*a*), but evidently extends at least from the proximal end of the girdle to the antapex. Its borders posteriorly are drawn out into projecting processes, one of which extends slightly beyond the antapex.

The nucleus and other cytoplasmic inclusions are not figured and no reference is made by Pouchet regarding these structures. The color of the organism, which he notes as similar to that of *G. spirale*, is probably greenish.

DIMENSIONS.—Length, 104$\mu$; transdiameter, 39$\mu$.

OCCURRENCE.—Figured by Pouchet (1885*a*) from collections made in the Atlantic off Concarneau, France, in June.

SYNONYMY.—Originally described by Pouchet (1885*a*) as a distinct species and also as a variety of *Gymnodinium spirale*. He wavered between these two conceptions in his discussion, introducing both designations in his text and inserting a query (?) after his varietal designations in his description of his figure. Lemmermann (1899) transferred it to *Spirodinium* as a species of that genus.

## **Gyrodinium crassum** (Pouchet)

Text figure CC, 21

*Gymnodinium crassum* Pouchet (1885*a*), pp. 66–67, pl. 4, fig. 28; (1885*b*), pp. 528, 529, pl. 26, fig. 2; (1887), p. 89; (1894), p. 169.
*G. crassum*, Bütschli (1885), pp. 965, 971.
*G. crassum*, Schütt (1895), p. 40.
*Spirodinium crassum*, Lemmermann (1899), p. 359.
*S. crassum*, Pavillard (1905), pp. 47, 80.
*S. crassum*, Paulsen (1908), p. 103, fig. 141.
*S. crassum*, Lebour (1917*b*), p. 195, fig. 12.

DIAGNOSIS.—A large species with long ellipsoidal body, its length 2.54 transdiameters; girdle a descending left spiral, displaced 0.92 transdiameter; sulcus extending from girdle to antapex; surface striate; color, yellowish brown. Length, 165$\mu$. Atlantic, Concarneau, France, in October; Plymouth Sound, England, in June; Arctic Ocean, Gulf of Lyons, October and November.

DESCRIPTION.—Body elongate ellipsoidal with irregular rounded apices, slightly wider posteriorly, its length 2.54 transdiameters at the widest part, which is about the middle of the hypocone. The epicone exceeds the hypocone in length by about 0.18 of its own length. It is long, with its sides subparallel to near the apex where they contract irregularly to the narrow, bluntly rounded apex. Its length on the left and right sides is about 0.38 and 0.73 respectively of the total length of the body. The hypocone is slightly wider than the epicone, and is more rounded towards the antapex, the left side of which is notched by the distal end of the sulcus.

The girdle is posterior to the equatorial plane for about 0.75 of its length. It meets the proximal end of the sulcus at a distance from the apex of 0.38 of the total length of the body. It sweeps around the body in a descending left spiral, its distal end joining the sulcus 0.73 of

the total length of the body from the apex, being displaced 0.89 transdiameter. The furrow is relatively narrow, 0.06 transdiameter, and deeply impressed with recessed anterior lips and rounded posterior border. The sulcus begins at the proximal end of the girdle and extends posteriorly to the antapex, as a narrow channel. Pores and flagella were not noted by Pouchet (1885*b*).

The nucleus is ovoidal and situated near the center of the body, but is not definitely shown in position in Pouchet's figures (1885*a*, *b*). The cytoplasm is filled with large vacuoles with a dark dense granular mass near its center. The surface is marked with broken (?) longitudinal striae. The color is yellowish brown with a darker mass near the center.

DIMENSIONS.—Length, 120μ to 200μ; transdiameter, 60μ to 65μ.

OCCURRENCE.—Figured by Pouchet (1885*a*, *b*) from the Atlantic off Concarneau, France, from collections made in October and (1894) from the Arctic Ocean near Spitzbergen. The other records of its appearance are as follows: Lebour (1917*b*) from Plymouth Sound, England, in June. The form she describes is considerably smaller than Pouchet's, having a length of only 75μ. Pavillard (1905) records it from the Gulf of Lyons in October and November.

SYNONYMY.—Originally described from a single individual by Pouchet (1885*a*) as *Gymnodinium crassum*, and again in the same year (1885*b*, pl. 26, fig. 2) he figures another individual assigned to *G. crassum* which differs from the first figure in the dimensions and the clear indication of a median longitudinal furrow without spiral course. His earlier figure (see his pl. 4, fig. 28) showed a lateral, furrow-like indentation on the left side (of the figure), which might be interpreted as indicating a spiral course of about 0.3 turn on the part of the longitudinal furrow. However, he speaks of this longitudinal furrow as being slightly undulating without specifying the course of the furrow which is hidden in the figure. The probabilities are that the notch does not represent a furrow and that the two figures refer to the same species. Both figures are inverted. Lemmermann (1899) and later Paulsen (1908) refer the species to *Spirodinium*.

COMPARISONS.—The cytoplasmic structure of this species recalls that of *Gymnodinium dogieli* and *G. pachydermatum*, without, however, having the thickened periplast or ectoplasmic region of that species. The dark mass near the center of the body is evidently formed of the dark, highly refractive granules similar to those found in *Gymnodinium*, and which are probably the metabolic products of holozoic nutrition.

*Gyrodinium crassum* is the largest species in *Gyrodinium* and significantly is one with a northern distribution, and found in the cooler part of the year. It is not close to any other species in the genus in proportions or structure. The nearest one appears to be *G. ochraceum* sp. nov. (fig. DD, 17), but the color of the latter is far more brilliant, its sulcus has more displacement and torsion, and the apices are different in the two species.

## **Gyrodinium culeus** sp. nov.

Plate 7, figure 77; text figure CC, 2

Diagnosis.—A medium sized species with ellipsoidal body, its length 1.71 transdiameters; girdle a submedian, descending left spiral, displaced 0.63 transdiameter; sulcus extending from apex to antapex; color, pearl grey with rose-red pigment granules. Length, 65μ. Pacific off La Jolla, California, August.

Description.—The body is subellipsoidal in outline, widest posteriorly, with broad apices, its length 1.71 transdiameters at the widest part, which is near the middle of the hypocone. The hypocone exceeds the epicone in size, its length being nearly equal but its transdiameter slightly greater than that of the epicone. The epicone is elongate hemispherical in shape, with symmetrically rounded sides. It is slightly notched at the apex by the proximal end of the sulcus. The right side widens somewhat behind the level of the anterior pore. It has a length on the left and right sides of 0.32 and 0.68 respectively of the total length of the body. The hypocone is elongate hemispherical in shape, slightly wider with sides more convex than those of the epicone. The antapex is smoothly rounded without sulcal notch.

The girdle is submedian in position. Its proximal end joins the sulcus at a distance from the apex of 0.32 of the total length of the body. It follows a descending left spiral course around the body and meets the sulcus at a distance from the apex of 0.68 of the total length of the body, its displacement being 0.63 transdiameter. It has a width of about 0.06 transdiameter and is deeply impressed wih smooth borders. The sulcus begins in a slight enlargement at the apex and extends posteriorly in an almost straight line to near the antapex. The anterior flagellar pore opens at the proximal junction of the girdle and sulcus, the posterior pore about one width of the girdle below their posterior junction.

The nucleus is a broadly ellipsoidal body, filled with fine, moniliform chromatin strands with a circular arrangement. It is found in the anterocentral part of the body. Its major and minor axes are about 0.55 and 0.44 transdiameters in length respectively.

A small, sacklike pusule opens into the anterior flagellar pore. None was noticeable at the posterior pore. The cytoplasm is finely granular and, in the individual figured, was densely filled with large vacuoles containing a salmon-pink fluid. No other bodies were present. The general color of the cytoplasm is a pearl grey, with a faint tinge of rose red. The latter color was condensed into a group of rose-red granules at the antapex and another group near the left margin of the body, immediately below the girdle. No striae or other surface markings could be detected.

Dimensions.—Length, 65μ; transdiameter, 38μ; axes of nucleus, 21μ and 17μ.

Occurrence.—One individual was taken August 8, 1917, 4 miles off La Jolla, California, in a haul from 80 meters to the surface and in a surface temperature of 21°9 C.

Comparisons.—The rose-red color of this form is the same as that found in *Gymnodinium rubrum* (pl. 8, fig. 86), *G. rubricauda* (pl. 8, fig. 88), *G. lineatum* (pl. 1, fig. 2), and *G. sulcatum* (pl. 8, fig. 83). The only *Gyrodinium* presenting the same coloring is *G. rubricaudatum* (pl. 10, fig. 116). Near it, however, is the coral red of *G. corallinum* (pl. 10, fig. 117) and *G. virgatum* (pl. 10, fig. 112).

The only non-striate *Gyrodinium* approaching this species in size and proportions is *G. dorsum* sp. nov. (fig. CC, 19), but this species differs from *G. culeus* in having less displacement of the girdle, which is also farther posterior.

## **Gyrodinium cuneatum** nom. sp. nov.

Text figure CC, 17

*Gymnodinium gracile,* Pouchet (1885*a*), pp. 69–71, pl. 4, figs. 32, 33.

DIAGNOSIS.—A large species with obovate or cuneiform body, its length 1.72 transdiameters; girdle a descending left spiral, displaced 0.6 transdiameter; sulcus extending from apex to antapex; epicone striate; color, rose. Length, 100μ. Atlantic off Concarneau, France.

DESCRIPTION.—The body is obovate or cuneiform in shape, widest anteriorly, its length 1.72 transdiameters at the widest part, which is at the girdle. The hypocone exceeds the epicone in size, being nearly twice its length. The epicone has the shape of a broad, low cone of about 100° with the apex slightly notched (by the anterior end of the sulcus?). It has a length on the left and right sides of 0.37 and 0.7 respectively of the total length of the body. The increase in length is confined to the right side of the ventral surface where it is drawn out posteriorly in a long slender point. The hypocone has an elongate campanulate shape, flaring at the region of the girdle and symmetrically rounded posteriorly.

The girdle is premedian for most of its length, with a distance from the apex at its proximal and distal ends of 0.37 and 0.7 respectively of the total length of the body, having a displacement of 0.6 transdiameter. It passes around the body in a transverse plane for about 0.75 of the circuit, turning posteriorly at a rapidly steepening angle which becomes about 15° with the longitudinal plane, at its point of union with the sulcus. The furrow has a width of about 0.06 transdiameter, and is deeply impressed with overhanging borders. The sulcus probably begins at the notch at the antapex and passes posteriorly as a slender, obscure trough in a nearly straight line to the antapex. The longitudinal flagellum arises a short distance beyond the distal junction of the girdle and sulcus. The transverse flagellum is not figured by Pouchet (1885*a*).

The nucleus is ellipsoidal and located near the posterocentral part of the body. Its major and minor axes are about 0.26 and 0.48 transdiameters respectively in length.

The central part of the cytoplasm is occupied by a mass of yellow-orange granules of varying sizes, larger in the center and smaller peripherally. Large colorless vacuoles are present in the epicone with a few in the antapical region. The general color of the body is a transparent rose diffused through the cytoplasm. The surface of the epicone is marked by longitudinal striae which fade out near the apex and girdle.

DIMENSIONS.—Length, 90–100μ; transdiameter, 58μ; axes of nucleus, 28μ and 17μ.

OCCURRENCE.—Figured by Pouchet (1885*a*) from the Atlantic off Concarneau, France.

SYNONYMY.—This form was figured by Pouchet as *Gymnodinium gracile* Bergh. It differs, however, from that species in its lack of a differentiated ectoplasm, absence of striae on the hypocone, and in the greater displacement of its girdle. This latter feature removes it from *Gymnodinium*, and we, therefore, place it in *Gyrodinium* as *G. cuneatum* nom. sp. nov.

### **Gyrodinium dorsum** sp. nov.

Plate 7, figure 81; text figure CC, 19

DIAGNOSIS.—A medium sized species with elongate ellipsoidal body, its length 1.83 transdiameters; girdle postmedian, a descending left spiral, displaced 0.43 transdiameter; color, yellowish. Length, 72μ. Pacific off La Jolla, California, August.

DESCRIPTION.—The body is elongate ellipsoidal with broad, rounded apices, nearly circular in cross-section, its length 1.83 transdiameters at the widest part, which is at the girdle. The epicone exceeds the hypocone in size, its length being greater by 0.31 of its own length. It is elongate hemispherical in size with symmetrically rounded sides and broad apex. It has a length on the left and right sides of 0.47 and 0.7 respectively of the total length of the body. The hypocone is hemispherical posteriorly with its sides very slightly elongate anteriorly and flaring around the anterior margin. It has a length on the left and right sides of 0.4 and 0.25 respectively of the total length of the body.

The girdle is postmedian in position for the greater part of its length. Its proximal end joins the sulcus at a distance from the apex of about 0.47 of the total length of the body. It sweeps around the body in a descending left spiral with its distal end meeting the sulcus at a distance from the apex of 0.7 of the total length of the body. The furrow has a width of 0.06 transdiameter, and is rather deeply impressed with smooth borders. The sulcus extends from near the apex to near the antapex in a slightly sinuous course. The furrow is deep and varies somewhat in width throughout its course. The anterior flagellar pore opens at the anterior junction of the girdle and sulcus, the posterior pore slightly posterior to the midpoint between the distal junction and the antapex.

The nucleus is spherical and is located in the posterior half of the body. It is densely filled with chromatin threads. Its axis is about 0.66 transdiameter in length.

A large sacklike pusule opens into each flagellar pore. The cytoplasm is finely granular. A large food mass, olive buff in color, occupied a position above the nucleus. Scattered through the peripheral layer of cytoplasm were numerous blue-green oil drops. The general color is aniline yellow mixed with grey and shading into buckthorn brown at both apices.

DIMENSIONS.—Length, 72μ; transdiameter, 39μ; axis of nucleus, 25μ.

OCCURRENCE.—A single individual was taken August 21, 1917, 5 miles off La Jolla, California, in a haul from 83 meters to the surface and in a surface temperature of 21°9 C.

SYNONYMY.—Pouchet's form (1883), *Gymnodinium spirale* var. *C,* is probably the same as our species. It is somewhat larger, 119μ as compared with 72μ in ours, but this is not too great for variations within the species. The girdle is postmedian and its displacement is about the same as in *Gyrodinium dorsum*. Its nucleus is spheroidal and in the plane of the posterior junction of the girdle and sulcus. It differs greatly from *G. spirale*, both in the size and shape of body and its lack of surface striae.

COMPARISONS.—In only two other species of *Gyrodinium* has the girdle become posteriorly located, *G. crassum* (fig. CC, 21), in which only a small portion is anterior to the midplane, and *G. glaucum* (fig. DD, 16), in which the hypocone is a relatively small part of the body.

## **Gyrodinium falcatum** nom. sp. nov.

Text figure CC, 11

*Gymnodinium fusus* Schütt (1895), in part, including only fig. 81, pl. 25.

DIAGNOSIS.—A large species with irregular, spindle-shaped body, its length 1.87 transdiameters; girdle submedian, a descending left spiral, displaced 0.39 transdiameter; sulcus short on both hypocone and epicone; yellow ochre chromatophores. Length, 121$\mu$. Atlantic (?) or Bay of Naples.

DESCRIPTION.—The body is irregularly spindle-shaped, concave dorsally, nearly straight ventrally, its dorsoventral and transverse diameters subequal, its length 1.87 transdiameters at the widest part. It is broadly rounded in the middle, and contracted into narrower processes at both ends. The epicone is slightly larger than the hypocone, its length being greater by 0.11 of its own length. It is roughly subconical in shape, rotund posteriorly, deeply contracted midway between the girdle and the apex, forming an irregular lobe anteriorly with convex sides with a width of 0.41 transdiameter and a truncate apex. It is somewhat asymmetrical with the anterior lobe slightly deflected to the right. It has a length on the left and right sides of 0.41 and 0.62 respectively of the total length of the body. The hypocone is less irregular than the epicone, rotund anteriorly with the posterior lobe shorter and the antapex more rounded than in the epicone.

The girdle is submedian in position, its proximal end joining the sulcus at a distance from the apex of 0.41 and its distal end 0.62 respectively of the total length of the body. It sweeps around the body in a descending left spiral course, displaced posteriorly 0.39 transdiameter. The furrow has a width of about 0.06 transdiameter, and is deeply impressed with smoothly rounded borders. The sulcus is short on both epicone and hypocone, is deeply impressed in the intercingular area, soon fading out towards both apices. The flagella and pores were not figured by Schütt (1895).

The body is completely filled with stout rodlike, yellow ochre chromatophores and spheroidal bodies closely crowded together. Nucleus and pusules were not figured by Schütt. The pellicle is double contoured. The organism was surrounded by a cyst which conformed to the shape of the body but was somewhat larger in size.

DIMENSIONS.—Length, 121$\mu$; transdiameter, 65$\mu$; length of cyst, 175$\mu$.

OCCURRENCE.—Figured by Schütt (1895) from material collected by the Plankton Expedition, presumably from the Atlantic or from the Bay of Naples.

SYNONYMY.—Schütt (1895) on his plate 24, figure 79 (our text figure X, 5), portrays *Gymnodinium fusus,* a form which is evidently a true *Gymnodinium.* On his plate 25, figure 81 (our text fig. CC, 11), he gives the same name to another organism which has the *Gyrodinium* type of girdle, with approximately the same size as the first form. While the comparative length and breadth may vary considerably in the species or even in the same individual, corresponding to different states of contraction and expansion, yet this does not affect the displacement of the girdle, the intercingular area remaining nearly constant. The girdle displacement in his second figure (our text fig. CC, 11) is greater than one-fifth the total length of the body; we therefore place it in the genus *Gyrodinium* as *G. falcatum.* Schütt's figure $81_2$, plate 25, is inverted, showing a reversed relation to that in his figures $81_1$ and $81_3$. The absence of the flagella

makes the orientation of this species a tentative one only. We have, however, followed, in our description, the orientation given in Schütt's figure $81_1$.

Comparisons.—This is one of the four species of *Gyrodinium* showing the presence of chromatophores, the other species being *G. pusillum* (Schilling), *G. melo* sp. nov., and *G. foliaceum* sp. nov. (figs. CC, 3, 9, 18). The yellow-ochre chromatophores of this species are similar to but smaller and more numerous than those in *Gymnodinium fusus*. The presence of small globules or vacuoles throughout the cytoplasm suggest holozoic nutrition, as these are probably products of metabolism. In its contracted apices this species is unique in *Gyrodinium*.

### **Gyrodinium fissum** (Levander)

Plate 9, figure 95; text figure DD, 8

*Gymnodinium spirale* var. *D* Pouchet (1883), p. 448, fig. K.
*G. fissum* Levander (1894*a*), pp. 43–50, pl. 2, figs. 5–20; (1894*b*), p. 210; (1900), p. 41; (1901*a*), pp. 8, 13, 18, 19; (1901*b*), p. 6; (1913), p. 36 (as *Spirodinium fissum*).
*Spirodinium fissum*, Lemmermann (1900), p. 116; (1901), p. 359; (1905*a*), p. 20.
*S. fissum*, Paulsen (1908), p. 101, fig. 139.
*Gymnodinium fissum*, Ostenfeld (1908), pp. 136, 162, 210, 213.
*Spirodinium fissum*, Lebour (1917*b*), p. 193.

Diagnosis.—A small species with subovoidal or ellipsoidal body, its length 1.79 transdiameters; girdle a descending left spiral displaced 0.31 transdiameter; sulcus extending from apex to antapex; surface finely striate; color, pale Veronese green. Length, 46μ. Pacific off La Jolla, California, July, August; Atlantic off Concarneau, France; Gulf of Finland.

Description.—The shape of the body is subovoidal to ellipsoidal, somewhat metabolic posteriorly, its length 1.79 transdiameters at the widest part, which is at the girdle. A cross-section of the body is nearly circular in outline. It is rounded at both apices, but usually more tapering anteriorly or the two may be subequal. The epicone exceeds the hypocone in size, its length being greater by 0.22 of its own length. The epicone is rounded dome-shaped, somewhat less than a hemisphere, with broad, symmetrically rounded apex. The relative length and width vary considerably in different individuals; when well extended it is subconical with slightly rotund sides. As the contraction of the body increases the convexity of the sides becomes more pronounced and the altitude decreases. It has an average length on the left and right sides of 0.4 and 0.67 respectively of the total length of the body. The hypocone is slightly broader than the epicone with broad, rounded antapex, or it may be equal or slightly narrower with the right side of the antapex extending farther posteriorly than the left side.

The girdle is submedian in position, its proximal end joining the sulcus at a distance from the apex of 0.4 of the total length of the body. It forms a descending left spiral with its distal end joining the sulcus at a distance from the apex of 0.67 of the total length of the body, its displacement being about 0.31 transdiameter. The greater part of this displacement takes place in the distal fourth of the girdle where it follows a course at an angle of about 45° with the median longitudinal plane. The first part of its course is in a nearly transverse direction around the body. The furrow has a width of about 0.08 transdiameter and is deeply impressed with smooth borders, of which the anterior one is deeply undercut. Both borders are usually raised

somewhat above the surface of the body. The sulcus begins near the right side of the apex and extends posteriorly in a slightly sinuous line to the antapex. The anterior flagellar pore opens at the proximal junction of the girdle and sulcus, the posterior pore about one width of the girdle below the distal junction.

The nucleus is a spheroidal body filled with coarse chromatin strands. It is found near the center or sometimes in the anterior part of the body. Its axis is about 0.5 transdiameter in length.

A small sacklike pusule opens into each flagellar pore; sometimes one or both may be temporarily absent. In one individual the anterior pusule was located near the center of the body and connected with the anterior pore by a slender canal. The cytoplasm is coarsely granular, often vacuolate in structure with few to many long, greenish rodlets radially arranged. The peripheral zone contains a layer of much smaller, radially arranged, blue-green rodlets placed at right angles to the surface. They appear between the surface striae in surface view as minute, blue-green, circular granules. The surface is longitudinally striate with equidistant, blue-green lines, about 24 across the ventral face of the epicone, and twice as many on the hypocone. The general color of the organism is pale Veronese green with, rarely, a tinge of coral red in the epicone.

DIMENSIONS.—Length, 46–57$\mu$; transdiameter, 29–38$\mu$; axis of nucleus, 13–17$\mu$.

OCCURRENCE.—This was first observed in two surface hauls made July 18 and 19, 1906, one 0.75 mile, the other 1.5 miles off La Jolla, California, with a No. 20 net, and in a surface temperature of 21°9 C. On July 12 and 20, 1917, it was taken in two hauls made with a No. 25 net, 6 miles offshore, from 80 meters to the surface and in surface temperatures of 20·6 C and 21°1 C respectively. It was again observed August 8, in a haul 4 miles offshore, from 80 meters to the surface and in a surface temperature of 22°5 C.

Other records of its occurrence are as follows: Pouchet (1883) from the Atlantic off Concarneau, France; Levander (1894*a*–1913), from the Gulf of Finland near Helsingfors, Finland; Ostenfeld (1908), from the Aral Sea in May, in surface temperature ranging from 17°7 C to 25°6 C, and Lebour (1917*b*), from Plymouth Sound, England, in August and September.

SYNONYMY.—This was first figured by Levander (1894*a*) as *Gymnodinium fissum* and was later changed by Lemmermann (1900) to *Spirodinium fissum*. In 1908 Paulsen placed with it as synonymous a form figured by Pouchet in 1883 as *Gymnodinium spirale* var. *D*. Ostenfeld (1908) records a species from the Aral Sea as *Spirodinium fissum* Levander with a question mark, stating that he was unable to identify it definitely as Levander's species. His observations were limited entirely to preserved material, and these forms very rarely withstand contact with a fixing fluid. Miss Lebour's (1917*b*) form from Plymouth Sound, England, is also doubtfully allocated. No figure or description is given save that it is yellow in color with a peculiar dorsoventral flattening. In all of our material the color was green and the body circular or nearly so in cross-section. In Levander's (1894*a*) description the color is green and the body rounded in vertical view. He observed one individual with a slight dorsoventral compression of the body.

Comparisons.—Levander (1894*a*) describes the long greenish rodlets in his figures as chromatophores. Such structures are frequently met with in the Gymnodiniidae, as in *Gymnodinium dogieli* (pl. 3, fig. 34) and *G. pachydermatum* (pl. 8, fig. 32), and, with a shorter length, in many others. These are probably metabolic in origin. On the dissolution of the cytoplasm they disappear, as do fluid-filled vacuoles, and our own observations lead us to believe that such is their structure, and that their function is concerned with the metabolism of the cell in other relations than as chromatophores.

## **Gyrodinium flavescens** sp. nov.

Plate 4, figure 39; text figure CC, 16

Diagnosis.—A small species with slightly asymmetrical, subovoidal body, its length 1.85 transdiameters; girdle a descending left spiral, displaced 0.81 transdiameter, with overhang of about 0.4 transdiameter; sulcus extending from near apex to antapex, with torsion of 0.4 transdiameter; color, aniline yellow. Length, 50$\mu$. Pacific off La Jolla, California, August.

Description.—The body is subovoidal and somewhat asymmetrical, its left dorsal side being convex and the right ventral slightly concave. In cross-section the body is nearly circular. It is widest posteriorly and its length is 1.85 transdiameters at the widest part. The length of the epicone exceeds that of the hypocone by 0.25 of itself. The epicone is convex on the right side and slightly concave on the left side with broad, rounded apex. It has a length on the left and right sides of 0.36 and 0.8 respectively of the total length of the body. The hypocone is hemispherical in shape, somewhat wider than the epicone and slightly notched by the distal end of the sulcus.

The proximal end of the girdle joins the sulcus at a distance from the apex of 0.36 of the total length of the body. It passes around the body in a descending left spiral, meeting the sulcus at 0.8 of the total length of the body from the apex, with a displacement of 0.81 transdiameter and an overhang of about 0.4 transdiameter. The furrow has a width of about 0.09 transdiameter and is deeply impressed, with smooth, rounded borders. The sulcus begins midway between the anterior flagellar pore and the apex. It extends posteriorly in a sigmoid curve with a torsion of about 0.35 to the antapex. Its width is about half that of the girdle, becoming narrower in front of the anterior flagellar pore and beyond the posterior pore. The anterior flagellar pore opens at the anterior junction of the girdle and sulcus, the posterior pore near the antapex.

The nucleus is a long, sausage-shaped body found in the left side. Its unusual length may, perhaps, be due to the oncoming of division. It was filled with long, moniliform chromatin strands lying in its long axis. Its axes were 1.3 and 0.3 transdiameters in length respectively.

The cytoplasm is coarsely granular, with numerous, minute, blue-green oil droplets scattered through its peripheral zone. Several yellowish citrine-colored bodies were present, probably food masses. The general color of the organism is aniline yellow shading to buckthorn brown, diffused throughout the cytoplasm. Minute, dark refractive granules are also abundant. No striae or other surface markings could be detected. A thin-walled, hyaline cyst, somewhat larger than the body, enclosed it.

DIMENSIONS.—Length, 50μ; transdiameter, 26μ; axes of nucleus, 36μ and 9μ.

OCCURRENCE.—A single individual was taken August 15, 1917, with a No. 25 silk net, 0.75 mile off La Jolla, California, in a haul from 80 meters to the surface and in a surface temperature of 21°9 C.

COMPARISONS.—This species, in the torsion of the girdle, foreshadows the *Cochlodinium* type of furrow arrangement. The overhang, however, is still considerably less than in that genus. There is no non-striate species of *Gyrodinium* which approaches it in proportions.

### **Gyrodinium flavidum** sp. nov.

Plate 7, figure 73; text figure CC, 20

DIAGNOSIS.—A large species with asymmetrical, rotund ellipsoidal body, its length 1.5 transdiameters; girdle a descending left spiral, displaced 0.54 transdiameter; sulcus extends from apex to antapex; color, ochraceous grey. Length, 102μ. Pacific off La Jolla, California, August.

DESCRIPTION.—The body is robust ellipsoidal, asymmetrical with the ventral face more convex than the dorsal face, its length 1.5 transdiameters at the widest part. A cross-section of the body is nearly circular in outline. The hypocone exceeds the epicone in size, its length being greater by 0.25 of its own length. The epicone is asymmetrical, the left side being raised in a high shoulder effect, throwing the apex, a knoblike extension, somewhat to the right. It has a length on the left and right sides of 0.16 and 0.51 respectively of the total length of the body. The hypocone is also asymmetrical, but less so than the epicone. Its sides are rounded and the antapex forms a short knoblike projection. It has a length on the left and right sides of 0.76 and 0.41 respectively of the total length of the body. The parts of both epicone and hypocone bordering the girdle are drawn out into wide, shelflike ridges.

The girdle is premedian in position for most of its course. Its proximal end joins the sulcus at a distance from the apex of 0.16 of the total length of the body. It sweeps around the body in a descending left spiral course to meet the sulcus at a distance from the apex of 0.51 of the total length of the body. The furrow has a width of about 0.07 transdiameter, and is deeply impressed, with borders raised somewhat above the surrounding surface of the body. The sulcus is a narrow trough extending in a slightly sinuous line from near the apex to near the antapex. The anterior flagellar pore opens at the anterior junction of the girdle and sulcus, the posterior pore midway between the distal junction and the antapex.

The nucleus is a spheroidal body found in the left side, slightly anterior to the equatorial plane. It is filled with moniliform, chromatin strands spirally arranged. Its axis is about 0.35 transdiameter in length.

The cytoplasm is coarsely granular, especially near the surface, giving the organism a mottled appearance. It was filled with large vacuoles of the same color as the surrounding cytoplasm, a pearl grey. Scattered throughout the cytoplasm but becoming much denser at the apices are minute granules of ochraceous orange and near the surface green oil droplets. Nutrition is evidently holozoic, as the cytoplasmic inclusions are probably the products of metabolism. A small sacklike pusule opens into the posterior flagellar pore. In other individuals one was present at the anterior pore also. No striae were detected on the surface.

DIMENSIONS.—Length, 102–118μ; transdiameter, 58–68μ; axis of nucleus, 25μ.

OCCURRENCE.—Two individuals were taken August 21, 1917, with a No. 25 silk net, 5 miles off La Jolla, California, in a haul from 63 meters to the surface and in a surface temperature of 21°9 C.

COMPARISONS.—In the outline of the body and the arrangement of girdle and sulcus this species resembles *G. truncus* sp. nov. (fig. DD, 4). Its lack of surface striae, however, differentiates it from that species and places it in the subgenus *Laevigella*. It is also different in its relatively shorter intercingular sulcus and its differentiated apical point. It is the most rotund representative in the subgenus *Gyrodinium*.

## **Gyrodinium foliaceum** nom. sp. nov.

Text figure CC, 18

*Gymnodinium viride* Schütt (1895), pl. 26, fig. 88.

DIAGNOSIS.—A small species with rotund ellipsoidal body, its length 1.2 transdiameters; girdle a descending left spiral, displaced 0.3 transdiameter; sulcus extending from girdle to antapex; green chromatophores. Length, 50μ. Atlantic or Bay of Naples.

DESCRIPTION.—The body is stout ellipsoidal, broadly rounded at both ends, its length 1.2 transdiameters at the widest part. The hypocone exceeds the epicone in length by about 0.15 of its own length. The epicone is subhemispherical with broad apex or the apex may be marked off by a slight pointed projection. It has a length on the left and right sides of about 0.18 and 0.54 respectively of the total length of the body. The hypocone is broad and rounded, somewhat less symmetrical than the epicone, and without sulcal notch.

The girdle joins the sulcus proximally about 0.18 of the total length of the body from the apex. It sweeps around the body in a descending left spiral course which becomes displaced posteriorly 0.3 transdiameter. The furrow is wide, 0.09 transdiameter, and deeply impressed with overhanging borders. The flagella and pores were not indicated by Schütt (1895). The sulcus begins at the girdle or it may arise at the apex. It extends posteriorly to the antapex in a sinuous line, but with no resulting torsion.

The nucleus is an ellipsoidal body in the posterior part. Its major and minor axes are 0.4 and 0.26 transdiameter in length respectively. A small sacklike pusule is present in the anterior part of the body connected with the region of the anterior pore by a slender canal. A few large, clear vacuoles are usually found in the cytoplasm, particularly in the epicone. Large, irregularly shaped, leaflike green chromatophores are found, sometimes near the middle of the body, in other cases filling the peripheral zone over the entire body.

DIMENSIONS.—Length, 50μ; transdiameter, 42μ; axes of nucleus, 17μ and 11μ.

OCCURRENCE.—Figured by Schütt (1895) from collections made by the Plankton Expedition, presumably from the Atlantic or from the Bay of Naples.

SYNONYMY.—This form was described by Schütt (1895) as *Gymnodinium viride* sp. nov. without knowing that this name had been used previously by Penard (1891) for a different species from fresh water. We therefore propose the new name *foliaceum* for it, and, by reason of its girdle, transfer it to the genus *Gyrodinium*.

COMPARISONS.—This species is close to *Gyrodinium melo* sp. nov. (fig. CC, 9), but is smaller, stouter, with less of an apical point, less displacement of girdle and torsion of sulcus with no overhang. The presence of chromatophores differentiates it definitely from *Gyrodinium ovoideum* sp. nov. (fig. CC, 6), a larger species without apical point but with about the same proportions.

### **Gyrodinium fucorum** (Küster)

Text figure EE, 3

*Gymnodinium fucorum* Küster (1908), pp. 352–356, figs. 1–4.
*G. fucorum*, Kofoid (1909), p. 246.
*G. fucorum*, Entz (1910), p. 161.
*G. fucorum*, Pavillard (1910), p. 536.
*G. fucorum*, Jollos (1910), pp. 181–193, pls. 7, 8.
*G. fucorum*, Günther (1911), p. 8.
*G. fucorum*, Hartmann (1911), p. 16, fig. 4.
*G. fucorum*, Senn (1911), p. 639.

DESCRIPTION.—A small species with rotund ellipsoidal body and broad apices, its length 1.33 transdiameters at the widest part; the girdle a descending left spiral, its relations to the sulcus unknown. The epicone exceeds the hypocone in size. The color is pale yellow. Küster's (1908) outline figures give the outline only of the cell, omitting all cell contents.

DIMENSIONS.—Length, 28–85$\mu$; transdiameter, 60–65$\mu$.

OCCURRENCE.—This was figured by Küster (1908) from the North Sea off Helgoland, Germany. He was able to keep it in cultures of sea water in the laboratory for six months.

SYNONYMY.—Under the name *Gymnodinium fucorum* Küster (1908) has figured a form with a spiral girdle which evidently belongs to *Gyrodinium*. His figures and diagnosis, however, are entirely inadequate to establish its species characters, giving as he does the merest outline of the body and omitting the full course of the girdle and its relations with the sulcus.

Jollos in 1910 published the results of his studies of the same material, which he obtained from Küster. Unfortunately he does not add to our knowledge of the species characters of this form beyond stating that the girdle forms a steep spiral. This character would remove it from *Gymnodinium*, where he leaves it, but is sufficient only to locate it in the genus *Gyrodinium*. He describes division which takes place within the cyst and results in four- or eight-celled stages (Küster, 1908). He also figures swarm spores, but does not show any connecting link between them and the dividing *Gymnodinium*. The later development of the swarm spores was not followed. It is possible that he is here confusing two entirely different organisms. His figures 30–41, plate 8, are those of a small flagellate belonging to *Bodo* or *Prowazekia*, having a nucleus with a central karyosome, a parabasal body or large blepharoplast and two unequal flagella, one of them trailing. This divides by a simple mitosis with a small number of chromosomes, unlike the type of mitosis found in *Gymnodinium*. There appear, therefore, fundamental differences between his two

groups of organisms too great to suggest any close relationship between them. The entire lack of any suggestive links between the two groups would tend to confirm our supposition that these are separate and distinct organisms. In view of the lack of definite species characters both in Küster's description and in that of Jollos we place this form among the species *incertae sedis* until it has been reinvestigated.

### **Gyrodinium fulvum** sp. nov.

Plate 7, figure 70; text figure DD, 9

Diagnosis.—A small species with ovoidal body with pointed apex, its length 1.87 transdiameters; girdle a descending left spiral with slight overhang and displacement of 0.9 transdiameter; sulcus extending from girdle to antapex; surface unevenly striate; color, yellow ochre. Length, 62μ. Pacific off La Jolla, California, July.

Description.—The body is ovoidal, rounded posteriorly, tapering abruptly anteriorly to a point, its length 1.87 transdiameters at the widest part below the girdle. In cross-section the body is nearly circular. The epicone and hypocone are subequal in size, though the greatest length of the epicone is about 0.32 greater than that of the hypocone. Its transdiameter is somewhat less. The epicone is broad and rotund posteriorly, tapering anteriorly to a slender, pointed apex nearly 2 girdle widths in length. It has a length on the left and right sides of 0.36 and 0.85 respectively of the total length of the body. The hypocone is elongate, subhemispherical with the antapex slightly notched ventrally by the distal end of the sulcus. It has a length on the left and right sides of about 0.59 and 0.19 respectively of the total length of the body.

The proximal end of the girdle joins the sulcus at a distance from the apex of 0.36 of the total length of the body. It follows a descending left spiral course around the body, its distal end meeting the sulcus at a distance from the apex of 0.85 of the total length of the body. Its displacement is about 0.9 transdiameter with an overhang of about 0.2 transdiameter. It has a width of about 0.07 transdiameter and is deeply impressed, undercutting its anterior border and smoothly rounding out to the posterior one. The sulcus extends from the girdle to the antapex in a slight sigmoid curve. Its width is nearly equal to that of the girdle. The anterior flagellar pore opens at the proximal junction of the girdle and sulcus, the posterior pore near the antapex.

The nucleus is a spheroidal body filled with loose chromatin strands. It is located near the center of the body. Its axis is about 0.48 transdiameter in length.

The pusule of the individual figured shows a rather unusual development. It consists of a large, globular vesicle nearly as large as the nucleus in the posterior part of the body, connected with the anterior flagellar pore by a long, slender canal. No pusule was present at the posterior pore. The cytoplasm is coarsely granular. In the peripheral zone are numerous small spherules, probably pigment, yellow ochre in color, with a few larger, greenish yellow bodies near the center of the body. The cytoplasm is pearl grey in color. The surface of the body is striate, with the number of lines on the hypocone about twice that on the epicone where there are about 22 across the ventral face. The latter differ also in that every other line is slightly heavier and broader than the intermediate lines.

Dimensions.—Length, 62μ; transdiameter, 33μ; axis of nucleus, 16μ.

Occurrence.—This was taken July 5, 1917, in a haul 6 miles off La Jolla, California, from 80 meters to the surface and in a surface temperature of 21°9 C.

COMPARISONS.—The small yellow-ochre spherule found in this species is probably pigment similar to that present in *G. ochraceum* (pl. 7, fig. 76). It did not show the same motility, but continued observation may establish its similarity in that respect also. It differs from *G. ochraceum* in its type of surface striae and in the smaller degree of torsion of the sulcus, with 0.1 as compared with 0.5 turns about the body. This species has the most highly developed apical point in the genus except for those of *G. fusiforme* nom. sp. nov. and *G. lachryma* (Meunier).

## **Gyrodinium fusiforme** nom. sp. nov.

Text figures EE, 4, 8

*Spirodinium fusus* Meunier (1910), p. 63, pl. 14, figs. 23–26.
Not *Gyrodinium falcatum* nom. sp. nov. (= *Gymnodinium fusus* Schütt (1895) in part).

DIAGNOSIS.—A small species with slender fusiform body, its length 3.7 transdiameters; girdle a descending left spiral, displaced 1.4 transdiameters; sulcus not determined. Length, 74μ. Arctic Ocean.

DESCRIPTION.—The body is slender fusiform, tapering to a sharp point at both apices, widest in the middle, its length 3.7 transdiameters at the widest part. The epicone and hypocone are subequal. The epicone is slender conical, about 30° anteriorly, slightly broader posteriorly, with a slender, acuminate apex. It has a length on the left and right sides of 0.29 and 0.71 respectively of the total length of the body. The hypocone is also slender conical, with a long attenuate antapex in the type figure (fig. EE, 4), somewhat shorter and blunter in a second specimen (fig. EE, 8).

The girdle is a descending left spiral with a distance from the apex at its proximal and distal ends of 0.29 and 0.71 transdiameters respectively. The furrow is not distinctly marked off in Meunier's figures, but it seems to have a width of about 0.18 transdiameter, and is shallow with rounded borders. The sulcus is imperfectly represented in the figures.

The nucleus is an ellipsoidal body filled with moniliform chromatin strands and lying in the central or anterior part of the body. Its major and minor axes are 0.8 and 0.5 transdiameters respectively.

Immediately posterior to the nucleus is a large vacuole. The peripheral zone of cytoplasm is filled with short rodlets apparently arranged at right angles to the surface.

DIMENSIONS.—Length, 74μ; transdiameter, 20μ; axes of nucleus, 16μ and 10μ.

OCCURRENCE.—This species was figured by Meunier (1910) from material collected by the Duke of Orleans's Arctic Expedition of 1907 in the Arctic Ocean near Nova Zembla.

SYNONYMY.—Meunier (1910) described his species as *Spirodinium fusus.* This name was preoccupied by *Gymnodinium fusus* Schütt (1895), under which designation two different forms were figured, one a *Gymnodinium, G. fusus* Schütt, and the other a *Gyrodinium, G. falcatum* nom. sp. nov., which we have separated from Schütt's species. We therefore change the specific name of Meunier's form to *fusiforme,* on the ground that the specific name *fusus* was once applied to a species which is now included within *Gyrodinium* (now *G. falcatum*).

## Gyrodinium glaucum (Lebour)

Plate 9, figure 94; text figure DD, 16

*Spirodinium glaucum* Lebour (1917*b*), p. 196, fig. 13.

DIAGNOSIS.—A small species with broadly fusiform body with abruptly contracted apices, length 2.46 transdiameters; girdle far posterior, a descending left spiral, displaced 0.26 of the total length; sulcus extending from the girdle to the antapex; color, greyish green. Length, 40μ. Pacific off La Jolla, California, July; Plymouth Sound, England, May to October.

DESCRIPTION.—This is a small species with fusiform body which tapers abruptly at both apices, nearly circular in cross-section, its length 2.46 transdiameters at the widest part. The girdle is placed far posteriorly, making the epicone occupy the larger portion of the body. The epicone has a length on the left of 0.67 and on the right of the sulcus of 0.9 of the total length of the body. The left side is more convex than the right. The apex is pointed and flexed to the left with a resulting rounding up of the right side. The hypocone is very short and rounded, abruptly tapering to the antapex, which is pointed and slightly excavated on the left side by the distal end of the sulcus.

The junction of the girdle and sulcus occurs at about 0.67 of the total length of the body from the apex. It passes around the body in a descending left spiral course and becomes displaced posteriorly on the right side about 0.64 transdiameter, of which the greater part occurs in the last third of its course. On the left side the girdle is wide, about 0.1 transdiameter, and in the last fourth of its course it narrows until at its distal end it is about 0.3 of its width at its beginning. It lies in a deep depression with smooth overhanging sides. The anterior flagellar pore is located at the proximal junction of the girdle and sulcus, the posterior pore at the distal one.

The sulcus is nearly straight, invading the epicone for a short distance anterior to the proximal end of the girdle and extending posteriorly to the antapex. It is relatively wide at its anterior end and becomes narrow near the antapex.

The nucleus is large and is located in the epicone. It is nearly spheroidal in outline with an axis of about 0.76 transdiameter. It is filled with moniliform chromatin strands lying obliquely to the longitudinal plane of the body.

The cytoplasm is clear and hyaline, pale greenish yellow in color. It is nearly filled with hyaline spherical granules, oil droplets and refractive bodies. There are also present 4 to 5 long, slender, tapering, yellowish green rodlets, about 0.5–0.66 of the total length of the body in length. These are parallel and are arranged longitudinally near the periphery of the body. They are probably products of metabolism, nutrition being holozoic. The surface is sparsely striate with longitudinal, equidistant striae, about 10 across the ventral face.

DIMENSIONS.—Length, 40μ; transdiameter, 16μ; nucleus, 12μ and 13μ.

OCCURRENCE.—This was figured by Lebour (1917*b*) from Plymouth Sound, England, where it was present from May to October. A single individual of this species was met with July 17, 1906, in a surface haul taken with a No. 8 net, 1.5 miles offshore, at San Diego, California, and in a surface temperature of 21°9 C.

ACTIVITIES.—The specimen under observation was restless, in constant motion, usually moving in a flat, anticlockwise spiral direction with a radius not to exceed twice its own length. The ventral surface was usually kept

uppermost with no rotation on the axis of the body. Occasionally there was a spasmodic rotation of the body in an anticlockwise spiral, rarely in the reverse direction, on its main axis. Not infrequently the organism would rise from the substrate and turn a somersault backward from the previous direction of progress and then resume the spiral gyrations.

SYNONYMY.—In Miss Lebour's figures she gives as surface striae what seems to correspond to the long, slender rodlets in our form. In her figure, 13*b*, these pass through the girdle, a condition never found in surface striae which terminate at or near the margins of the girdle. In her figures the anterior end of the body is occupied by a large, yellow mass, which is usually though not always present, and the nucleus is posteriorly placed. This large food mass (?) was absent in our example with the nucleus anterior and the cytoplasm filled with small spherules. These differences are not great enough to separate the two forms.

COMPARISONS.—This species shows the greatest extreme in the relative proportions of epicone and hypocone, the latter being comparatively minute. The general tendency from *Amphidinium*, with its relatively minute epicone, up through *Gymnodinium* and *Gyrodinium*, has been towards an equalization of the two parts of the body with a slight leaning towards a greater size in the hypocone. These conditions are reversed in *G. glaucum,* as also to a much smaller extent in *G. crassum* (fig. CC, 21) and *G. dorsum* (fig. CC, 19).

## **Gyrodinium grave** (Meunier)

Text figure DD, 7

*Spirodinium grave* Meunier (1910), p. 64, pl. 14, figs. 27, 28.

DIAGNOSIS.—A small species with stout ellipsoidal body, its length 1.29 transdiameters; girdle a descending left spiral, displaced 0.6 transdiameter, constricting the body; sulcus extending from anterior end of girdle to near antapex; surface finely striate. Length, 57μ. Arctic Ocean off Nova Zembla.

DESCRIPTION.—Body stout ellipsoidal, with broadly rounded apices, widest in the middle, its length 1.29 transdiameters at the widest part. The epicone and hypocone are subequal. The epicone is subhemispherical in outline, with a length on the left and right sides of 0.24 and 0.7 respectively of the total length of the body. The hypocone is broadly rounded with broad, slightly flattened antapex.

The girdle in Meunier's figure (1910, pl. 14, fig. 27, reproduced in our text figure DD, 7) is not complete in its proximal end. This has been completed in our figure by the slender lines. It joins the sulcus at a distance from the apex of about 0.24 of the total length of the body. It sweeps around the body in a descending left spiral of 1.25 turns, displaced posteriorly 0.6 transdiameter. It is wide, about 0.09 transdiameter, and deeply impressed with rounded borders. The sulcus extends from the proximal to the distal end of the girdle. It probably has a longer extension posteriorly at least. Flagella are lacking in the figures given.

The nucleus is a large subspheroidal body found in the center of the organism. Its axis is about 0.5 transdiameter in length. It is filled with coarse, chromatin strands. The surface is

covered with longitudinal equidistant lines, apparently equal in number on both epicone and hypocone, about 30 across the ventral face. It is probable that they have more of a spiral course than figured by Meunier.

DIMENSIONS.—Length, 57µ; transdiameter, 44µ; axis of nucleus, 22µ.

OCCURRENCE.—Figured by Meunier (1910) as a rare species from the collections made by the Duke of Orleans's Arctic Expedition of 1907 from the Arctic Ocean near Nova Zembla.

SYNONYMY.—Originally described by Meunier (1910) as *Spirodinium grave*, but is transferred by us to *Gyrodinium*.

COMPARISONS.—In the torsion of the body *G. grave* is nearest to *G. intortum* sp. nov., a non-striate species of similar size and proportions, but with much more recorded torsion of the sulcus anteriorly. This furrow is not figured by Meunier anterior to the girdle. Otherwise the species is unique in the genus in form and torsion.

We have inverted Meunier's (1910, pl. 14, fig. 27) figure and have completed, as faint lines crossing the striae, the probable course of the distal end of the girdle to its junction with the sulcus. Our reasons for this change in orientation are the facts that the proximal end of the girdle is usually the best developed region, the distal end the least, in cases of modification in the course of the girdle. In Meunier's figures the animal is oriented with the proximal end deficient. We turn the figure end for end and thus bring this deficient section to the distal end.

### **Gyrodinium herbaceum** sp. nov.

Plate 10, figure 109; text figure DD, 6

DIAGNOSIS.—This is a small species with subovoidal body, its length 2.11 transdiameters; girdle a descending left spiral, displaced one transdiameter; sulcus short above and below junctions with girdle, with a torsion 0.5 turn; surface finely striate; color, deep lichen green. Length, 38µ. Pacific off La Jolla, California, July.

DESCRIPTION.—The body is subovoidal, widest near the middle, its length 2.11 transdiameters at the widest part. In cross-section it is nearly circular. The epicone is exceeded in size by the hypocone, though its greatest length is 0.16 greater than that of the hypocone. The epicone is subconical (60°) in shape, convex on the left and concave on the right side with a blunt, rounded apex. Its length on the left and dorsal sides is about 0.32 of the total length of the body. Near the right lateral margin of the body its length becomes greater, reaching posteriorly in a slender point on the right side of the sulcus for about 0.78 of the total length of the body. The hypocone is broader than the epicone, its sides are more convex and the antapex broad and rounded.

The proximal end of the girdle joins the sulcus at a distance from the apex of 0.32 of the total length of the body. For the first half of its course it passes around the body in a nearly transverse direction, then turns posteriorly in a steeply descending spiral and forms an angle of about 35° with the median longitudinal plane of the body at its junction with the girdle at a distance from the apex of 0.78 of the total length of the body. Its displacement is about one

transdiameter. The furrow has a width of about 0.08 transdiameter, and is deeply impressed with smooth sides. The sulcus extends but a short distance on the epicone and posteriorly it fades out a short distance beyond its distal junction with the girdle. It turns towards the left posteriorly with a torsion of about 0.5 turn. The anterior flagellar pore is found at the anterior junction with the girdle, the posterior pore at the posterior junction.

The nucleus is spheroidal in shape and is located slightly above the central portion of the body. It is filled with coarse, moniliform chromatin strands. Its axis is about 0.66 transdiameter in length.

A large sacklike pusule opens into the anterior flagellar pore. The cytoplasm is clear and transparent and contains many large blue-green oil drops, and dark refractive granules. In the individual figured a large, green food mass was enclosed in a food vacuole, evidence of holozoic nutrition. The surface of the body is striate with numerous, equidistant, blue-green striae, about equal in number on the hypocone and epicone, 18 to 20 across the ventral face. The color is a deep lichen green with tones of pearl grey. The whole organism has a highly refractive, glassy appearance.

DIMENSIONS.—Length, 38$\mu$; transdiameter, 18$\mu$; diameter of nucleus, 12$\mu$.

OCCURRENCE.—A single individual was taken July 13, 1917, with a No. 25 net, 1.25 miles off La Jolla, California, in a haul from 50 meters to the surface and in a surface temperature of about 20°1 C.

ACTIVITIES.—It was in constant motion under the microscope, moving in large circles counterclockwise, without rotation.

COMPARISONS.—This species presents certain similarities in its girdle and sulcus arrangement to *G. ochraceum* (pl. 7, fig. 76; fig. DD, 17), having the same amount of torsion but a slightly greater relative degree of displacement. It differs from that species in its smaller size, greenish color and lack of pigment, the possession of which is one of the most striking characteristics of *G. ochraceum*. In size and proportions it is near *G. viridescens* sp. nov. (fig. DD, 11), which has a much smaller epicone, and lacks the posterior torsion of the sulcus.

## **Gyrodinium hyalinum** (Schilling)

Text figure CC, 15

*Gymnodinium hyalinum* Schilling (1891), pp. 60, 61, pl. 3, fig. 14; (1891*b*), pp. 199–208, pl. 10, figs. 1–22; as *Spirodinium hyalinum* (1913), p. 21, fig. 2.

*G. hyalinum,* Ludwig (1898), p. 299.

*G. hyalinum,* Mez (1898), p. 216.

*G. hyalinum,* Zacharias (1899), p. 144.

*G. hyalinum,* Schönichen and Kalberlah (1900), p. 231; (1909), p. 252.

*Spirodinium hyalinum,* Lemmermann (1900), p. 116; (1903), p. 260; (1910), pp. 565, 613, 627, figs. 24, 27, 31.

*Gymondinium hyalinum* Entz, Jr. (1902), p. 125; (1907), p. 17; (1909), p. 254.

*G. hyalinum,* Wesenberg-Lund (1904), p. 107.

*G. hyalinum,* Ruttner (1906), p. 6.

*G. hyalinum,* Dogiel (1906), pp. 32, 40.

*G. hyalinum,* Klebs (1912), pp. 391, 429, 430.

*Spirodinium hyalinum,* West (1916), p. 53, fig. 36*c*.

Diagnosis.—A minute species with asymmetrical, ovoidal body, its length 1.36 transdiameters; girdle a descending left spiral, displaced 0.35 transdiameter; sulcus extending from girdle to antapex; no chromatophores. Length, 23.6$\mu$. Fresh-water ponds in the Botanical Gardens at Basel, Switzerland.

Description.—The body is irregularly ovoidal and widest in the middle, with broadly rounded but asymmetrical apices, its length 1.36 transdiameters at the widest part. The hypocone exceeds the epicone in extent, its length being greater by 0.27 of its own length. The epicone is broadly rounded at the apex and has a length on the left and right sides of 0.17 and 0.44 respectively of the total length of the body. It is oblique upon the right side. The hypocone is hemispherical in outline in the posterior half, with broad antapex, but slightly oblique upon left side.

The left side of the girdle is placed far anteriorly, meeting the sulcus at 0.17 of the total length of the body from the apex. It passes transversely around to the dorsal side, where it turns posteriorly in a descending left spiral course, displacing the right side of the girdle 0.35 transdiameter. The furrow is wide, about 0.23 transdiameter, and is deeply impressed with wide, overhanging borders. Its anterior border on the right side of the body projects considerably beyond the posterior lip and is less rounded. The sulcus extends from the middle of the ventral side to the posterior end of the body, but its position is not shown in Schilling's (1891*a*, *b*, 1913) figures. The transverse flagellum traverses the entire length of the girdle, arising presumably at the proximal junction of the girdle and sulcus. The longitudinal flagellum arises slightly behind the distal end of the girdle.

Nucleus and pusules are not figured by Schilling. A small carmine-colored stigma is present in the sulcal region near the origin of the longitudinal flagellum. Nutrition is holozoic. Schilling (1891*b*, pl. 10, figs. 5–7, 9–22) has described a process of food taking for this species, in which amoeba-like pseudopods are formed to aid in the ingestion of small organisms. Unfortunately, however, the connecting links between the *Gymnodinium hyalinum* and the amoeba-like forms are lacking in his figures.

Dimensions.—Length, 23.6$\mu$; transdiameter, 20.7$\mu$, as given in the text (Schilling, 1891*a*, *b*, 1913). A careful measurement of his figure, however, gives the transdiameter as 17.3$\mu$. In the description above we have used the latter measurement.

Occurrence.—Figured by Schilling (1891*a*) from fresh-water ponds in the Botanical Gardens at Basel, Switzerland.

Synonymy.—Originally described by Schilling (1891) as *Gymnodinium hyalinum*, this species was later transferred by Lemmermann (1900, 1903) to *Spirodinium*. Schilling (1913) later accepted this allocation in his monograph of German fresh-water dinoflagellates.

Comparisons.—This species and *G. pusillum* form the only fresh-water representatives in the genus. They greatly resemble each other in the position of girdle, size, and shape. *G. hyalinum* lacks the chromatophores present in *G. pusillum*.

### **Gyrodinium intortum** sp. nov.

Text figure CC, 10

Diagnosis.—A small species with broadly ellipsoidal body, its length 1.37 transdiameters; girdle a descending left spiral, displaced 0.4 transdiameter, with an overhang of 0.6 transdiameter; sulcus with antapical loop and torsion of 1 turn; color, green. Length, 62$\mu$. Pacific off La Jolla, California, July.

Description.—The body is broadly ellipsoidal with broad apices, circular in cross-section, its length 1.37 transdiameters at the widest part. The epicone and hypocone are subequal, the epicone having a length greater by 0.12 of its length, but its transdiameter is less than that of the hypocone. The epicone has a length from the proximal and distal ends of the girdle of about 0.4 and 0.69 respectively of the total length of the body. It is irregularly convex-conical with broad, rounded apex. The hypocone has a slightly greater transdiameter than the epicone, broad posteriorly, subtruncate with a broad, shallow sulcal notch.

The girdle is a descending left spiral of 1.6 turns with a displacement of 0.4 transdiameter. Its distance from the apex at its proximal and distal ends is about 0.4 and 0.69 respectively of the total length of the body. Its course for the proximal and distal thirds of its length is nearly transverse, the greatest posterior deflection occurring in the middle third on the dextrodorsal surface of the body. The furrow is relatively narrow, its width about 0.04 transdiameter, deeply impressed, the excavation undercutting both borders slightly.

The sulcus invades the epicone in a long apical loop which encircles the apex and terminates on the sinistrodorsal surface some distance posterior to the apex. The sulcus continues its spiral course beyond the anterior junction with the girdle, with a sinistro deflection of 0.6 transdiameter in the intercingular area before meeting the distal end of the girdle. Posteriorly it passes directly to the antapex, where it forms a broad, shallow notch. The furrow is shallow and slightly more than half as wide as the girdle. Posterior to the distal junction it becomes deeply impressed, with the right border drawn out into a flap which nearly covers the channel. The anterior flagellar pore opens at the proximal junction of the girdle and sulcus, the posterior pore midway between the distal one and the antapex. It lies at the apex of the angle formed by the right border of the sulcus and the furrow. The transverse flagellum traverses the entire length of the girdle.

The nucleus is an ellipsoidal body lying in the posterior part of the body near the distal junction of the girdle and sulcus. Its major and minor axes are 0.44 and 0.33 transdiameter respectively in length.

The cytoplasm is very clear and transparent, its granular structure scarcely perceptible. The anterocentral part of the body is filled with a large food mass showing traces of a dinoflagellate girdle, olive yellow in color with smaller, slightly darker granules of the same color. The peripheral layer of cytoplasm is marked by a reticulum of vetiver green with a background of pale glaucous green. Nutrition is holozoic.

Dimensions.—Length, 62μ; transdiameter, 45μ; axes of nucleus, 20μ and 15μ.

Occurrence.—This was observed on July 20, 1917, 6 miles off La Jolla, California, in a haul from 80 meters to the surface and in a surface temperature of 21° C.

Comparisons.—This is one of the most aberrant species in the genus *Gyrodinium*. Its sulcus strikingly resembles that found in *Pouchetia* (as in *P. maculata* (pl. 11, fig. 119) and *P. schuetti* (fig. PP, 10) in its well developed apical loop, and is quite unlike that found elsewhere in the genus *Gyrodinium*. Its length of girdle, amount of girdle displacement, and lack of an ocellus leaves no doubt as to its status generically. In its reticulate peripheral zone it resmbles *Cochlodinium clarissimum* (pl. 5, fig. 60).

It belongs in the subgenus *Laevigella*, though it is not closely related to any other member of that group.

### **Gyrodinium lachryma** (Meunier)

Text figure EE, 6

*Spirodinium lachryma* Meunier (1910), p. 63, pl. 14, figs. 21, 22.

Diagnosis.—A medium sized species with ovoidal body, its length 2.83 transdiameters; girdle a descending left spiral, displaced 1.4 transdiameters; sulcus extending from the anterior end of girdle to antapex. Length, 105μ. Kara Sea off Nova Zembla, July.

Description.—The body is ovoidal, broadly rounded posteriorly and gradually tapering to a slender point anteriorly, its length 2.83 transdiameters at the widest part. The epicone exceeds the hypocone in length by 0.42, but its narrower width makes their relative proportions nearly equal. It is slender conical anteriorly (25°) with a narrow, pointed apex and expanding to about 66° in the region of the girdle. It has a length on the left and right sides of 0.45 and 0.90 respectively of the total length. The hypocone is subhemispherical posteriorly with a broad, rounded antapex.

The girdle meets the proximal end of the sulcus at a distance from the apex of 0.45 of the total length of the body. It follows a steeply descending left spiral course around the body and meets the distal end of the sulcus about 0.9 of the total length of the body from the apex, being displaced posteriorly 1.4 transdiameters. The furrow is not well marked out in Meunier's (1910) figures, but its width seems to be about 0.19 transdiameter and it is rather shallow. The flagella are also omitted from his figures. The sulcus begins at the proximal end of the girdle and extends posteriorly to near the antapex.

The nucleus is large, ellipsoidal and is found in the center of the body with its major axis parallel to the long axis of the body. Its major and minor axes are about 0.9 and 0.4 transdiameter in length respectively. It is filled with loose chromatin strands following its longer axis. The peripheral zone of cytoplasm is filled with small, closely crowded rodlets arranged radially in longitudinal rows. Color?

Dimensions.—Length, 105μ; transdiameter, 37μ; axes of nucleus, 34μ and 14μ.

Occurrence.—Figured as a rare species by Meunier (1910) from the collections of the Duke of Orleans's Arctic Expedition of 1907 from the Kara Sea off Nova Zembla, July 30, in a haul from a depth of 127 meters.

Comparisons.—This species is close to *G. contortum* (Schütt) (fig. CC, 22), but differs from it in its more tapering epicone, more rotund hypocone, less torsion, and wider intercingular area.

### **Gyrodinium longum** (Lohmann)

Text figure DD, 10

*Cochlodinium longum* Lohmann (1908), p. 264, pl. 17, fig. 22.
*C. longum,* Paulsen (1908), p. 104, fig. 144.
*C. longum,* Ostenfeld (1913), p. 338.

Diagnosis.—A rather small species with slender subfusiform body, its length 2.69 transdiameters; girdle a descending left spiral, displaced 1.06 transdiameters; surface striate; color, light yellow. Length, 70μ. Baltic Sea off Kiel, Germany, June.

DESCRIPTION.—The body is irregularly fusiform, widest anteriorly, its length 2.68 transdiameters at the widest part, which is in the lower epicone. The epicone exceeds the hypocone in length by 0.25 of its own length. It is conical anteriorly (45°) with a blunt apex. It has a length on the left and right sides of 0.37 and 0.56 respectively of the total length of the body. The hypocone narrows behind the girdle to about 0.5 the width anteriorly. The antapex is obliquely truncate with a small knoblike projection from the center of the truncate surface.

The girdle begins at a distance from the apex of about 0.37 of the total length of the body. It passes around the body in a descending left spiral direction and terminates at a distance from the apex of 0.56 of the total length of the body, being displaced 1.06 transdiameters. The furrow is wide, about 0.1 transdiameter, and quite shallow. The sulcus is not shown in Lohmann's (1908) figure.

The nucleus is an ellipsoidal body near the center of the organism. Its major and minor axes are about 0.7 and 0.53 transdiameter in length respectively. The other cytoplasmic inclusions are very sparse and include three brownish food masses and several minute spherules. The surface of the body is covered with parallel longitudinal striae of granules linearly arranged, about 13 across one face. Unfortunately the striae are not shown in our figure as converging towards the apex as in Lohmann's original figure. The color of the body is light yellow.

DIMENSIONS.—Length, 70μ; transdiameters, 26μ; axes of nucleus, 18μ and 13μ.

OCCURRENCE.—Figured by Lohmann (1908) from collections made in the Baltic Sea off Kiel, Germany, in June.

DISCUSSION.—This species was originally described by Lohmann (1908) as *Cochlodinium longum*. His figure, however, does not show the characteristic *Cochlodinium* arrangement of girdle, that is, with the torsion of the body giving the girdle a length of at least 1.5 turns around the body. Neither is it possible with the furrows as drawn to force a *Cochlodinium* interpretation of the species. On the contrary, there seems to be a total lack of torsion with the girdle making but one spiral turn around the body. His figure also seems to be inverted with the girdle of the two faces drawn as though both parts were on the upper surface. In the reproduction of his figure, given herewith in our text figure DD, 10, these changes embodying our interpretation are incorporated, bringing his figure into conformity with other species of *Gyrodinium*. We therefore place Lohmann's species tentatively in the genus *Gyrodinium* as *Gyrodinium longum* (Lohmann).

It is quite possible that the drawing of this species is not inverted, and that a whole turn or more of the girdle is omitted in Lohmann's drawing, in which case the species is a *Cochlodinium*. Few, if any, *Gyrodinium* have the epicone so pronouncedly larger than the hypocone as it is in *G. longum* as we orient the body.

## **Gyrodinium maculatum** sp. nov.

Plate 6, figure 62; text figure DD, 19

DIAGNOSIS.—A medium sized species with ellipsoidal body, its length 1.49 transdiameters; sulcus extending from below the apex to antapex; girdle a premedian, descending left spiral, displaced 0.36 transdiameter; surface finely striate; violet pigment in epicone. Length, 61μ. Pacific off La Jolla, California, July, August.

DESCRIPTION.—The body is broadly ellipsoidal with broadly rounded, faintly subconical apices, its length 1.49 transdiameters at the widest part, which is below the girdle. A cross-section is nearly circular in outline. The hypocone exceeds the epicone in size, its length being greater by 0.2 of the total length. The epicone is rounded conical in shape, with broad, smoothly rounded apex. It has a length on the left and right sides of 0.21 and 0.57 respectively of the total length of the body. The hypocone has a length on the left and right sides of 0.73 and 0.4 of the total length of the body. Its sides are somewhat more convex than those of the epicone and taper more towards the antapex, which is usually narrower than the apex. The right side of the body has a slightly greater convexity than the left side.

The girdle is premedian in position for the greater part of its course. Its proximal end joins the sulcus at a distance from the apex of 0.21 and its distal end 0.57 respectively of the total length of the body. The first 0.5 transdiameter of its course follows an almost transverse direction around the body, beyond which it turns posteriorly in a gradually steepening angle which becomes about 45° with the longitudinal plane of the body, at its junction with the sulcus. The furrow has a width of about 0.06 transdiameter and is deeply impressed, undercutting the lip on the anterior side and sloping gradually out to the posterior lip. The sulcus begins below the apex and extends posteriorly to near the antapex in a sinuous, slightly sigmoid curved line. It begins as a shallow trough and deepens through the intercingular part of its course, becoming shallow distally and fading out near the antapex. The anterior flagellar pore opens at the anterior junction of the girdle and sulcus, the posterior pore about one width of the girdle below the distal junction.

The nucleus is a relatively large, spheroidal body filled with coarse, moniliform chromatin strands, which lie in the longitudinal plane. It is situated in the anterior part of the body or immediately dorsad from the intercingular region. Its axis is about 0.48 transdiameter in length.

Large, sacklike pusules are usually present at either or both pores. The cytoplasm is very finely granular, clear, and transparent. Food inclusions are usually present in the body, indicating a holozoic mode of nutrition. In the individual figured a large mass, buffy citrine in color, filled the posterior part of the body immediately behind the nucleus. A few minute refractive granules were scattered through the cytoplasm near the nucleus. The cytoplasm is pearl grey in color.

The most striking feature of this organism is its pigmented coloration. This is found in the cuticular layer and along the lines of striae. The surface is closely beset with equidistant, longitudinal lines, having a very faint, fluorite violet color. These are about 2.5 times as numerous on the hypocone as on the epicone, where there are 15 across the ventral face. They are further marked, generally throughout their entire length, by minute granules, fluorite violet in color, strung along the lines like beads on a string. The number of these varies slightly in different individuals and they are frequently scanty in the antapical region. In addition to these the peripheral zone in the epicone contains large agglomerated masses of the same pigment. The color of these larger masses is frequently so deep as to appear almost black when viewed under the low powers of the microscope. This pigment evidently has the same power of movement as that found in *Gymnodinium lineopunicum* and *Gyrodinium ochraceum*.

DIMENSIONS.—Length, 61–73μ; transdiameter, 41–54μ; axis of nucleus, 20–22μ.

OCCURRENCE.—The first specimen was taken July 5, 1904, 12 miles off Point Loma, California, with a No. 20 silk net, in a haul from 355 meters to the surface. It was again met with July 3, 1916, in a surface haul made at the end of the pier at the Biological Station at La Jolla, California. Throughout July and August, 1917, it was present in most of the hauls made at La Jolla, both in surface hauls and in the deeper hauls made farther offshore. The individual

figured was taken August 18, 4 miles offshore, from 80 meters to the surface and in a surface temperature of 20°2 C.

Activities.—These are active little forms in constant motion until slowed down by the adverse conditions found under the microscope. They move about in a loose spiral with a slow, clockwise rotation, varied with short periods of rapid whirling with the dorsal side uppermost.

Comparisons.—This is one of the few species below *Pouchetia* which possess pigment capable of active movement, and is probably near the line of evolution of that genus. The other members of *Gyrodinium* which are aligned with it in this respect are *G. ochraceum, G. corallinum,* and *G. virgatum.* In its girdle arrangement this species shows a close relationship with *G. fissum* (fig. DD, 8), *G. corallinum* (fig. DD, 12), and *G. pingue* (fig. DD, 15). The surface striae are also like those of *G. corallinum* and *G. fissum.*

## **Gyrodinium melo** sp. nov.

Plate 5, figure 50; text figure CC, 9

Diagnosis.—A medium sized species with rotund ovoidal body, its length 1.42 transdiameters; girdle a descending left spiral, displaced 0.53 transdiameter; sulcus extending from apex to antapex; color, grey with green chromatophores. Length, 66$\mu$. Pacific off La Jolla, California, July.

Description.—The body is rotund ovoidal, rounded posteriorly, tapering slightly anteriorly, its length 1.42 transdiameter at its widest part, which is equatorial in location. In cross-section the body is circular in outline. The hypocone exceeds the epicone in size, having a slightly greater length and a continuously greater transdiameter. The epicone has rounded sides and a short bluntly acuminate apex. It has a length on the left and right sides of 0.19 and 0.53 respectively of the total length of the body. The hypocone is elongate hemispherical with a symmetrically rounded antapex.

The girdle is a descending left spiral with a displacement of 0.53 transdiameter and an overhang of about 0.25 transdiameter. Its proximal end joins the sulcus at a distance from the the apex of 0.19 of the total length of the body. For the first 0.5 transdiameter of its course its direction is transverse beyond which it turns posteriorly on the dorsal face at an angle of about 55°, joining the sulcus distally about 0.53 of the total length of the body from the apex. The furrow has a width of about 0.06 transdiameter and is deeply impressed with smooth borders. The sulcus invades the epicone nearly to the apex and extends posteriorly to within a short distance of the antapex in a sigmoid line. It is rather shallow and fades out near the apices. The anterior flagellar pore opens at the proximal junction of the girdle and sulcus, the posterior pore about two widths of the girdle below the distal junction.

The nucleus is a large spheroidal body filled with coarse, moniliform chromatin strands. It is located dorsad to the intercingular area. Its axis is about 0.34 transdiameter in length.

The cytoplasm is coarsely granular and contains food masses, vacuoles, and a few minute, refractive granules. In the posterior part of the individual figured is a large, orange-rufous body, with a smaller body, brighter red in color, lying near it. In the anterior part of the body are three large vacuoles, one filled with a blue fluid, the others with a grey fluid. The general color of the cytoplasm is grey with darker tones in the peripheral zone. This zone also contains the irregular, leaflike, apple-green chromatophores. Nutrition is possibly both holophytic and holozoic, as the presence of both chromatophores and food bodies in the cytoplasm may indicate.

Dimensions.—Length, 61–67$\mu$; transdiameter, 43–47$\mu$; transdiameter of nucleus, 19$\mu$.

Occurrence.—Two individuals only of this species were observed. The first was taken on July 21, 1917, in a surface haul at the end of the pier at the Biological Station at La Jolla, California, with a No. 25 silk net. The second individual was taken July 22 at the same place and with the same apparatus.

Comparisons.—The coincident presence of chromatophores and food bodies, evidence of both holozoic and holophytic nutrition, is not an unknown phenomenon in the Gymnodinioidae. The same thing is found in *Amphidinium steini* (Stein, 1883, pl. 17, figs. 14–16), *Gymnodinium flavum* sp. nov., *G. ravenescens* sp. nov., *G. fulgens* sp. nov., and *G. herbaceum* sp. nov. (figs. X, 7, 21, 30; Y, 17). The presence of chromatophores is relatively rare in this genus, only three other species possessing them, *G. falcatum* sp. nov., *G. foliaceum* sp. nov., and *G. pusillum* (Schilling) (fig. CC, 11, 18, 3). It is close to *G. foliaceum* (fig. CC, 18), but is larger, with more displacement of the girdle and torsion of the body.

## **Gyrodinium mitra** nom. sp. nov.

Text figure EE, 5

*Gymnodinium spirale* var. *mitra,* Schütt (1895), pl. 21, fig. 68*a*.
*Spirodinium spirale* var. *mitra,* Lemmermann (1899), p. 359.

Diagnosis.—A rather small species with an asymmetrical subfusiform body, its length 2.6 transdiameters; girdle a descending left spiral, displaced 1.17 transdiameters; sulcus joining ends of girdle. Length, 78$\mu$. Atlantic or Bay of Naples.

Description.—The body is asymmetrical subfusiform, with a greater convexity on the right side of the epicone, tapering towards both apices, its length 2.6 transdiameters at the widest part which is anterior. The epicone exceeds the hypocone in size, its transdiameter being slightly greater and its length greater by 0.15 of itself. It is asymmetrical, the right side convex and the left nearly longitudinal, throwing the narrowly rounded apex strongly to the left. It has a length on the left and right sides of 0.29 and 0.75 respectively of the total length of the body. The hypocone is also asymmetrical, with a sigmoid outline on the left side, nearly straight on the right, throwing the antapex towards the right, but with less deflection than in the apex. It is narrower than the epicone with a slender blunt antapex.

The girdle is a descending left spiral distant from the apex at its proximal and distal ends about 0.29 and 0.75 respectively of the total length of the body. It is displaced about 1.17 transdiameters with a slight overhang. Its proximal end turns abruptly posteriorly at an angle of 50° with the longitudinal plane of the body, until it reaches the left lateral border where it turns and passes across the dorsal face in an almost transverse direction, turning again posteriorly near the right lateral margin and traversing the right ventral face at an angle of about 55° with the longitudinal plane. The furrow has a width of about 0.14 transdiameter and is deeply impressed with smooth borders. The sulcus in Schütt's (1895) figure does not extend beyond the intercingular region where its width is nearly equal to that of the girdle.

The nucleus is a rather large, ellipsoidal body, densely filled with short chromatin strands and located in the anterocentral part of the body. Its major and minor axes are about 0.75 and 0.5 transdiameters in length respectively.

The peripheral zone of cytoplasm is filled with short rodlets, presumably arranged at right angles to the surface, as in other species, but these are not figured by Schütt, who also omits oil vacuoles in the cytoplasm. Color?

DIMENSIONS.—Length, 78μ; transdiameter, 30μ; axes of nucleus, 23μ and 17μ.

OCCURRENCE.—Figured by Schütt (1895) from material collected by the Plankton Expedition, presumably from the Atlantic or from Bay of Naples.

SYNONYMY.—This was figured by Schütt (1895) as *Gymnodinium spirale* var. *mitra* and changed by Lemmermann (1899) to *Spirodinium spirale* var. *mitra*. It lacks the characteristic striate surface of *spirale*, however, and is also distinct from that species in its proportions; hence it can hardly be regarded as a variety of that species. We therefore propose for it specific rank under Schütt's varietal name.

## **Gyrodinium obtusum** (Schütt)

Plate 9, figure 103; text figure DD, 3

*Gymnodinium spirale* Bergh var. *obtusa* Schütt (1895), pl. 22, fig. 70.
*Spirodinium spirale* var. *obtusum*, Lemmermann (1899), p. 359.
*S. spirale* var. *obtusa*, Schröder (1900), p. 13.
*G. spirale* var. *obtusum*, Lebour (1917*b*).
Not *Gymnodinium spirale* var. *obtusum* Dogiel (1906), pp. 38–43, pl. 2, figs. 50–56 (= *Gymnodinium heterostriatum* nom. sp nov.).

DIAGNOSIS.—A medium sized species with ellipsoidal subsymmetrical body, its length 1.75 transdiameters; girdle a descending left spiral, displaced one transdiameter; sulcus extending from apex to antapex; surface finely striate with broken striae; color, amber yellow. Length, 70μ. Pacific off La Jolla, California, July; Atlantic, Gulf of Naples, Plymouth Sound, Englnd.

DESCRIPTION.—The body is moderately broadly ellipsoidal with broad, rounded apices, widest in the middle, its length 1.75 transdiameters at the widest part. A cross-section of the body is nearly circular in outline. The hypocone is slightly larger than the epicone, though the posterior deflection of a triangular portion of the epicone on the right ventral face gives it a greater length than the hypocone. The epicone is convex conical (75°) with broad, blunt apex. It has a length on the left and right sides of 0.22 and 0.80 respectively of the total length of the body. The greatest increase in its length is made on the right side of the ventral face where the distal border forms an angle of 45° with the longitudinal plane. The hypocone is somewhat broader than the epicone with a broader, more blunt antapex. It has a length on the left and right sides of the body of 0.18 and 0.72 respectively of the total length of the body.

The girdle forms a steeply descending left spiral, displaced one transdiameter or 0.57 of the total length of the body. Its proximal end joins the sulcus at a distance from the apex of 0.22 and its distal end 0.8 of the total length of the body. The first 0.5 transdiameter of its course is in a transverse plane, the remainder a gradually steepening spiral which forms in the last 0.5 transdiameter, an angle of 45° with the longitudinal plane of the body. The furrow has a width of about 0.06 transdiameter and is deeply impressed, its concavity undercutting the anterior border and sloping gradually out to the posterior one. The sulcus extends from the apex to the antapex in a nearly straight line. The trough is narrower than the girdle, shallow on the epicone,

becoming deeper in the intercingular area and the antapical region. The anterior flagellar pore is located at the anterior junction of the girdle and sulcus, the posterior pore about one width of the girdle below the distal junction.

The nucleus is an ellipsoidal body filled with coarse, moniliform subparallel chromatin strands in the posterocentral part of the body. Its major and minor axes are about 0.64 and 0.35 transdiameter in length respectively.

The sacklike pusule at the anterior pore is connected by a long tubular canal with the pusule at the posterior pore, the whole structure forming a complete channel between the two openings. The cytoplasm is finely granular and diffusely amber yellow in color. In the peripheral zone are numerous, short, slender blue-green rodlets or rhabdosomes arranged at right angles to the surface. In a surface view these appear as minute blue-green circles. The surface is finely striate with equidistant blue-green striae composed of linear series of short dashes, about 28 across the ventral face of the epicone. These are about twice as numerous on the hypocone as on the epicone.

DIMENSIONS.—Length, 70$\mu$; transdiameter, 39$\mu$; axes of nucleus, 25$\mu$ and 14$\mu$.

OCCURRENCE.—This species was first observed July 12, 1903, in a surface haul off La Jolla, California. It was met again July 9 and 11, 1917, in hauls 4 miles off shore, from 80 meters to the surface and in a surface temperature of 19°8 C.

Other records of the occurrence of this species are as follows: Schütt (1895) figures it from the material of the Plankton Expedition, presumably from the Bay of Naples or the Atlantic. Schröder (1900) lists it from the Gulf of Naples, and Lebour (1917*b*) records it from Plymouth Sound, England.

SYNONYMY.—Originally figured by Schütt (1895, pl. 22, fig. 70) as *Gymnodinium spirale* Bergh var. *obtusa* and later transferred by Lemmermann (1899) to *Spirodinium* by reason of its spiral girdle. Dogiel (1906) describes a *Gymnodinium* under this name, specifying neither new species nor Schütt as authority. His form is not, however, that which Schütt (1895) has figured. It is larger, has greater contrast in the intervals between the ribs in the epicone and hypocone, a straighter longitudinal furrow, and very little displacement of the distal end of the girdle below the proximal. This is 0.42 of the total length in Schütt's figure and only 0.05 in Dogiel's. The latter must therefore belong in *Gymnodinium*. It appears to be identical with our *Gymnodinium heterostriatum*.

COMPARISONS.—A peripheral zone of short rodlets is not uncommon in both *Gyrodinium* and *Gymnodinium* and is probably related to the metabolism of the cell. These are most marked in *Gyrodinium fissum* (fig. DD, 8) and *G. postmaculatum* (fig. DD, 20). The long radial rodlets are also repeated in *Gymnodinium pseudonoctiluca*, *G. dogieli* (pl. 3, fig. 34), *G. pachydermatum* (pl. 3, fig. 32), and *G. amphora* (pl. 3, fig. 26). These are not present in all individuals of the species and are probably related to certain stages of metabolism.

This species is close to *G. fissum* (Levander) (fig. DD, 8), but is yellow instead of green, has much greater displacement of girdle, and broken lines in its striae instead of continuous ones.

## **Gyrodinium ochraceum** sp. nov.

Plate 7, figures 76, 82; text figure DD, 17

Diagnosis.—A large species with bullet-shaped body, its length 2.28 transdiameter; girdle a descending left spiral with overhang of 0.4 transdiameter and displacement of 1.04 transdiameters; sulcus extending from apex to antapex in a left spiral of 0.5 turn; surface striate; color, ochraceous orange. Length, 123μ. Pacific off La Jolla, California, July.

Description.—The body is of robust habit, circular in cross-section; bullet-shaped with pointed anterior end, rounded posteriorly, its length 2.28 transdiameters at the widest part which is postmedian. The sides may be subparallel (pl. 7, fig. 76) or the dorsal surface may be convex and the ventral concave (pl. 7, fig. 82). The epicone and hypocone are subequal in size, though the greatest length of the epicone exceeds that of the hypocone by 0.24 of its own length. The epicone is elongate conical in outline, about 60° above the anterior pore, with convex sides and pointed apex. Its length on the left of the sulcus is about 0.35 and on the right is 0.87 of the total length of the body. Along the girdle it flares out abruptly into a narrow shelflike projection. The hypocone is dome-shaped with broadly rounded antapex. Like the epicone it forms a narrow, shelflike projection along the posterior border of the girdle. There is no sulcal notch at the postmargin.

The junction of the girdle and sulcus occurs at a distance from the apex of about 0.35 of the total length of the body. It forms a descending left spiral which is displaced posteriorly on the right side about 1.04 transdiameters, with an overhang of about 0.4 transdiameter. It lies in a wide, deep depression with wide overhanging, shelflike borders. The anterior flagellar pore is located at the anterior junction of the girdle and sulcus and the posterior pore midway between the posterior junction and the antapex.

The sulcus begins at or near the apex and extends to the antapex in a spiral course. Below the anterior pore it widens, contracts just above the distal junction and posteriorly expands into a wide trough which reaches the antapex, making 0.5 turn of a left spiral to the opposite face. It lies in a deep depression with high, smoothly rounded borders.

The nucleus is subspherical or slightly ellipsoidal and located in the middle regions on the right side of the body. It is filled with coarse, moniliform chromatin strands. Its axis is 0.5 transdiameter in length.

A long pusule, variously lobed and branched, opened into both flagellar pores, the expanded portions being connected by a long slender canal. The cytoplasm is clear and transparent and yellowish grey in color. Food inclusions of any kind were extremely rare in all the individuals of this species observed. The surface is finely striate with equidistant blue-green lines. These are about 2μ apart at the girdle, about 25 across the ventral face, and are approximately equal in number on epicone and hypocone. The general color of the body is yellow green with ochraceous-orange granules thickly scattered in the surface cytoplasm. This colored pigment possesses remarkable powers of amoeboid activity. In the first specimen observed it was collected in rounded granules scattered thickly over the surface with a mass in the apical region (pl. 7, fig. 76). Later these became grouped on the dorsal surface and along the region of the girdle, forming a wide band similar to that observed in another individual. The second individual was found in the same material with the color massed in a long bandlike zone with irregular margins, following the girdle around the body. After an hour and a half on the slide under observation, the edges of the band became more ragged and small particles were pinched off. These rounded up and moved out over the surface. Two hours later the entire pigment mass had thus become broken up into small granules evenly distributed over the body. Another individual was observed in which the small pigment granules were in the act of becoming agglomerated along the girdle into one long band.

DIMENSIONS.—Length, 110–123$\mu$; transdiameter, 45–55$\mu$; axis of nucleus, 21–22$\mu$.

OCCURRENCE.—Two individuals were taken July 12, 1917, 6 miles off La Jolla, California, with a No. 25 net, in a haul from 80 meters to the surface and in a surface temperature of 20° C. The following day it was observed in a haul taken with the same apparatus 1.25 miles offshore and from 50 meters to the surface. On July 20 it was taken in a haul 6 miles offshore and on July 27 at 4 miles off La Jolla. These were taken with the same apparatus, from 80 meters to the surface and in surface temperature of 20°5 C and 21°4 C respectively. It was fairly abundant in this material, seven individuals being observed in a short examination of the last haul.

ACTIVITIES.—These organisms are rather slow in their movements, moving around in large clockwise circles with anticlockwise rotation, changing the direction by a sudden jerk from right to left, sometimes turning in this manner fully 90° or slightly more, and continuing in a new spiral.

COMPARISONS.—The most remarkable feature of this organism is the amoeboid activity of the pigment, resembling, in this respect, *Gymnodinium punicum*, and foreshadowing the condition established in *Pouchetia* and *Erythropsis*. Other species, as *Gyrodinium maculatum*, show the presence of mobile pigment, but this is less active in these species in its movements.

In its type of structure and proportions this species stands near *G. spirale* (fig. DD, 14). The latter, however, shows a total lack of pigmentation. In its girdle arrangement it stands near the border line between *Gyrodinium* and *Cochlodinium*. The greater amount of torsion of the sulcus occurs posteriorly to the intercingular space as contrasted with its occurrence in the intercingular space in *Cochlodinium*. It stands near *G. contortum* (Schütt) (fig. CC, 22) of the subgenus *Laevigella* in the wide displacement and overhang of its girdle, resulting from the torsion of the intercingular sulcus.

The motility of its yellow-ochre pigment finds its parallel in *Gymnodinium lineopunicum* and in the amoeboid-pigment masses of the more highly specialized genera, *Pouchetia* and *Erythropsis*. In all of these, however, the pigment shows some shade of red or black, this species being distinct in the possession of a yellow-ochre pigment.

### **Gyrodinium ovatum** (Gourret)

Text figure EE 7

*Gymnodinium ovatum* Gourret (1883), p. 88, pl. 1, fig. 22.

DIAGNOSIS.—A small species with fusiform body, its length 2.88 transdiameters; girdle a descending left spiral, displaced 0.92 transdiameter; sulcus extends from the girdle to the antapex; color, yellow. Length (?). Gulf of Marseilles, France.

DESCRIPTION.—The body is slender fusiform with rounded apices, its length 2.88 transdiameters at the widest part. The epicone greatly exceeds the hypocone in extent, its length being greater by 0.46 of its own length. It has a length on the left and right sides of 0.51 and 0.87 of the total length of the body. The dorsal side is somewhat less symmetrical than the ventral, tapering more abruptly to the narrow, rounded apex. The hypocone is broader posteriorly than the epicone with broad, rounded antapex.

The girdle lies almost entirely posterior to the equatorial plane of the body. It meets the sulcus at a distance from the apex of 0.51 of the total length of the body. It follows a descending left spiral course around the body, displaced about 0.92 transdiameter, its distal end joining the sulcus about 0.12 of the total length of the body from the antapex. The sulcus extends from the proximal end of the girdle to the antapex as a rather deep furrow.

The nucleus is a small, spherical body found in the median ventral part of the cytoplasm. It is homogenous with clear, central, hyaline nucleolus. The body figured here by Gourret (1883) is unlike the nuclei found throughout the Gymnodinioidae both in relative size and structure and is probably a vacuole. The central part of the cytoplasm is granular and filled with oil droplets, with a hyaline zone near the periphery. The organism is yellow in color.

DIMENSIONS.—No dimensions are given by Gourret and the magnification of his figure could not be determined.

OCCURRENCE.—Gourret (1883) figured this species from the Gulf of Marseilles, France.

SYNONYMY.—This form was described by Gourret as *Gymnodinium ovatum*. Its girdle arrangement excludes it from that genus and it is here placed with *Gyrodinium* as *G. ovatum* (Gourret).

COMPARISONS.—This species is near *G. contortum* (Schütt), but differs from it in having a displacement of the girdle of about 0.33 of the total length as compared with 0.5 in *G. contortum*.

## **Gyrodinium ovoideum** sp. nov.

Plate 9, figure 106; text figure CC, 6

DIAGNOSIS.—A rather large species with rotund ellipsoidal body, its length 1.28 transdiameters; girdle a descending left spiral, displaced 0.37 transdiameter; sulcus extending from girdle to antapex; color, dilute primuline yellow. Length, 72μ. Pacific off La Jolla, California, May to August.

DESCRIPTION.—The body is stout, rotund ellipsoidal with broadly rounded apices, circular in cross-section, its length 1.28 transdiameters at the widest part. The epicone and hypocone are subequal in size. The epicone is subhemispherical in outline, its size smoothly rounded and apex broad. It has a length on the left and right sides of 0.34 and 0.61 respectively of the total length of the body. The hypocone is also subhemispherical in shape without sulcal notch at the antapex, its length nearly approximating that of the epicone.

The girdle is submedian in position, its proximal and distal ends meeting the sulcus at a distance from the apex of 0.34 and 0.61 respectively of the total length of the body. It forms a descending left spiral with its distal end displaced 0.37 transdiameter, and with a slight overhang. The furrow has a width of about 0.07 transdiameter and is deeply impressed with smooth rounded borders. The sulcus may invade the epicone for a short distance or may stop with the proximal margin of the girdle. It extends posteriorly in a sinuous line as a shallow trough which fades out near the antapex. The anterior flagellar pore is located at the proximal junction of the girdle and sulcus, the posterior pore slightly posterior to the distal junction.

The nucleus is ellipsoidal in shape and located in the anterocentral region. Large, moniliform chromatin strands traverse its longer axis. Its major and minor axes are about 0.5 and 0.4 transdiameter in length respectively.

A large sacklike pusule opens into each flagellar pore. The cytoplasm is granular and often contains a large, reddish-brown food mass, with numerous blue-green and small refractive spherules. These latter inclusions indicate a holozoic mode of nutrition. Striations and other surface markings could not be detected. The general color of the organism is dilute primuline yellow mixed with pearl grey and orange, diffused throughout the cytoplasm.

DIMENSIONS.—Length, 45–74$\mu$; transdiameter, 34–60$\mu$; axes of nucleus, 29–33$\mu$ and 23–24$\mu$.

OCCURRENCE.—The first individual was taken May 31, 1904, in a surface haul 9 miles off La Jolla, California. On June 24, 1917, it was found in the surface haul taken at the end of the pier at the Biological Station at La Jolla. It was also taken August 10 1 mile offshore in a haul from 50 meters to the surface and on the 15th 0.75 mile offshore in a haul from 83 meters to the surface.

COMPARISONS.—This species is near *G. ovum* (Schütt) ( fig. CC, 8), but is large with relatively much less displacement of the girdle, more symmetrical hypocone, and shorter sulcus.

## **Gyrodinium ovum** (Schütt)

Text figure CC, 8

*Gymnodinium ovum* Schütt (1895), pl. 25, fig. 23.
*G. ovum,* Calkins (1901), p. 118, fig. 64 A.

DIAGNOSIS.—A small species with ellipsoidal body, its length 1.4 transdiameters; girdle a descending left spiral, displaced 0.6 transdiameter; sulcus extending from girdle to antapex; color (?). Length, 28$\mu$. Atlantic (?) or Bay of Naples.

DESCRIPTION.—The body is broadly ellipsoidal with broad, rounded apices, its length 1.4 transdiameters at the widest part, which is at the middle. The epicone exceeds the hypocone in size, its length being greater by 0.11 of its own length. It is elongate, subhemispherical in shape, with broad, rounded apex. It has a length on the left and right sides of 0.32 and 0.68 respectively of the total length of the body. The hypocone is slightly less symmetrical than the epicone and notched on the left side of the antapical region by the distal end of the sulcus.

The girdle is submedian in position, its proximal end joining the sulcus at a distance from the apex of 0.32, its distal end 0.68 respectively of the total length of the body, forming a descending left spiral displaced 0.6 transdiameter. The furrow has a width of about 0.12 transdiameter and is rather shallow. The sulcus begins at the girdle and extends posteriorly in a sinuous line to the antapex. The flagellar pores were not figured by Schütt, though he shows the distal ends of both the transverse and longitudinal flagella.

The nucleus is an ellipsoidal body filled with coarse chromatin strands and lying in the right central part of the body. Its major and minor axes are about 0.62 and 0.37 transdiameter in length respectively.

The cytoplasm is filled with small spherules and contains besides these, vacuoles, and one large, spheroidal, brownish food mass, evidence of a holozoic mode of nutrition. The periplast of the body is double contoured in Schütt's figure. Color?

DIMENSIONS.—Length, 28μ; transdiameter, 20μ; axes of nucleus, about 10μ and 6μ.

OCCURRENCE.—Figured by Schütt (1895) from material of the Plankton Expedition from the Atlantic or Bay of Naples.

SYNONYMY.—The name *Gymnodinium ovum* as applied to this species by Schütt is now inapplicable, as the organism presents the *Gyrodinium* type of girdle.

COMPARISONS.—This species belongs with two other rather small, broadly ellipsoidal, non-striate marine species, *G. capsulatum* sp. nov. and *G. foliaceum* nom. sp. nov. (figs. CC, 14, 18). It is smaller than either of these, has relatively more displacement of the girdle and greater antapical asymmetry. It lacks the apical point found in *G. foliaceum*.

## **Gyrodinium parvulum** (Schütt)

Text figure CC, 4

*Gymnodinium parvulum* Schütt (1895), pl. 25, fig. 84.

DIAGNOSIS.—A minute species with subovoidal body, its length 2.2 transdiameters; girdle a descending left spiral, displaced 0.88 transdiameter; sulcus (?). Length, 33μ. Atlantic (?) or Bay of Naples.

DESCRIPTION.—The body is subovoidal, widest anteriorly and tapering at both ends, its length 2.2 transdiameters at the widest part, which is at the girdle. The hypocone exceeds the epicone in size, being nearly three times as large. The epicone is short, conical (90°) anteriorly with a blunt apex. Its length on the left and right sides is 0.20 and 0.36 respectively of the total length of the body. The hypocone is more tapering and slightly narrower at the antapex, which is without sulcal notch.

The girdle begins at a distance from the apex of 0.2 of the total length of the body. It follows a descending left spiral course around the body and terminates at a distance from the apex of about 0.4 of the total length of the body. The furrow is wide, about 0.23 transdiameter, and deeply impressed with overhanging borders. The sulcus and flagella are not shown in Schütt's (1895) figure.

The nucleus is an ellipsoidal body found in the anterodorsal part of the organism. Its major and minor axes are about 0.8 and 0.4 transdiameter in length respectively. It is densely filled with coarse chromatin strands. Two large brownish food masses occupy the posterior part of the body. The remainder of the cytoplasm is thickly strewn with vacuoles of varying sizes.

DIMENSIONS.—Length, 33μ; transdiameter, 15μ; axes of nucleus, about 12μ and 6μ.

OCCURRENCE.—A single specimen of this species has been recorded by Schütt (1895) from collections made by the Plankton Expedition from the Atlantic or the Bay of Naples.

COMPARISONS.—This species is nearest *G. pusillum* (Schilling and *G. hyalinum* (Schilling), both fresh-water species of smaller size and relatively larger epicone.

## **Gyrodinium pepo** (Schütt)

Text figure DD, 2

*Gymnodinium spirale* var. *pepo* Schütt (1895), p. 112, pl. 21, figs. $69_{1-3}$.
*Spirodinium spirale* var. *pepo*, Lemmermann (1899), p. 359.

Diagnosis.—A medium sized species with ovoidal flask-shaped body with contracted curved apex, its length 1.6 transdiameters; girdle a descending left spiral, displaced 0.54 transdiameter; sulcus extending from apex to antapex, surface coarsely striate. Length, 81μ. Atlantic (?) or Bay of Naples.

Description.—The body is stout ovoidal, widest posteriorly and tapering anteriorly, its length 1.6 transdiameters at the widest part, which is in the middle of the hypocone. The epicone is slightly longer than the hypocone, but is much narrower. It has a length on the left and right sides of 0.39 and 0.7 respectively of the total length of the body. The epicone contracts towards the apex which is deflected towards the left side of the body with the left side of the epicone concave and the right side convex. The hypocone is hemispherical behind the girdle region with broad, smoothly contoured antapex.

The proximal junction of the girdle and sulcus occurs at 0.39 of the total length of the body from the apex. It sweeps around the body in a descending left spiral course and joins the sulcus distally about 0.7 of the total length of the body from the apex, having a displacement of 0.54 transdiameter. The furrow is wide, 0.08 transdiameter, and deeply impressed with smooth borders. The sulcus begins near the apex and extends posteriorly to within a short distance of the antapex. The transverse flagellum arises at the anterior junction of the girdle and sulcus and traverses the entire length of the girdle. The longitudinal flagellum arises slightly below the posterior junction of the sulcus and girdle.

The nucleus is broadly ellipsoidal, and is located in the anterior part of the body. Its major and minor axes are about 1.56 and 0.40 transdiameters respectively. Coarse chromatin strands fill the body of the nucleus. A large pusule is found in the posterior part of the hypocone, but its connection with the posterior flagellar pore is not indicated. The cytoplasm is filled with large vacuoles, closely crowded together. In the peripheral layer are minute spherules, longitudinal, equidistant and about equal in number on both epicone and hypocone, about 24 across the ventral face. Color?

Dimensions.—Length, 81μ; transdiameter, 50μ; axes of nucleus, 28μ and 20μ.

Occurrence.—Figured by Schütt from the collections of the Plankton Expedition from the Atlantic or the Bay of Naples. A single specimen was taken, 1.25 miles off La Jolla, California, July 25, 1906, with a No. 20 net, in a surface haul.

Synonymy.—This species was figured by Schütt as *Gymnodinium spirale* var. *pepo*. and later changed by Lemmermann (1899) to *Spirodinium spirale* var. *pepo*. It has none of the characteristics of *spirale*, however, lacking the slender fusiform shape of body, the wider displacement of the girdle, and the slight torsion of the sulcus and body of that species. It cannot thus be considered a variety of that species and we therefore propose for it species rank, as *G. pepo*.

Comparisons.—This species has the most rotund inflated hypocone found in the genus. This feature, together with the curved apex, differentiates the

species from all others in the genus. The nearest approach to it is found in *G. lachryma* (Meunier), a much more attenuate and slender species, whose surface structure is unknown.

## **Gyrodinium pingue** (Schütt)

Plate 4, figure 38; text figure DD, 15

*Gymnodinium spirale* var. *pinguis* Schütt (1895), pl. 21, fig. 65.
*Spirodinium spirale* var. *pingue,* Lemmermann (1899), p. 359.

DIAGNOSIS.—A small species with elongated ovoidal body, its length 1.88 transdiameter; girdle a descending left spiral, displaced 0.74 transdiameter; sulcus extending from near apex to antapex; surface finely striate; color, pale lumiere green. Length, 51$\mu$. Pacific off La Jolla, California, July; Atlantic or Bay of Naples.

DESCRIPTION.—The body is ovoidal, circular in cross-section, broadly rounded posteriorly, narrowly so anteriorly, its length 1.88 transdiameters at the widest part in the upper hypocone. The hypocone exceeds the epicone in size, having a continuously broader transdiameter, though the lengths are approximately the same. The epicone is convex conical, forming an angle of about 70°, with a blunt apex. It has a length on the left and right sides of 0.25 and 0.66 respectively of the total length of the body. The hypocone is elongate hemispherical posteriorly with a broad antapex. It has a length on the left and right sides of 0.68 and 0.27 of the total length of the body.

The girdle is a descending left spiral with its proximal and distal ends joining the sulcus at a distance from the apex of 0.25 and 0.66 respectively of the total length of the body. In the first 0.5 transdiameter of its course its direction is slightly deflected anteriorly, turning posteriorly on the dorsal surface and continuing on the ventral surface in a steep spiral with its distal end displaced 0.74 transdiameter. The furrow has a width of about 0.09 transdiameter, and is deeply impressed with smoothly rounded borders. The sulcus extends from or near the apex posteriorly to the antapex in a slightly sinuous line. Its width is about half that of the girdle and is rather shallow, fading out near the antapex.

The nucleus is spherical in shape and is located at or near the center of the body. It is filled with fine moniliform chromatin strands. Its axis is about 0.4 transdiameter in length.

A large, sacklike pusule opens into the posterior flagellar pore, and is sometimes present at both pores. The cytoplasm is usually dense and alveolar in structure, often containing many inclusions, such as greenish refractive spherules, blue-green oil droplets and larger food masses indicative of holozoic nutrition. A peripheral zone of short, blue-green rodlets is often present. The color of the cytoplasm is pale lumiere green diffused throughout. The surface is finely striate, the striae varying somewhat in different individuals. In most of the specimens examined these consist of blue-green, equidistant lines. In other forms the lines may be broken by minute blue-green granules strung along their length like beads on a thread or giving the appearance of a dot and dash (pl. 4, fig. 38).

DIMENSIONS.—Length, 45–51$\mu$; transdiameter, 30–27$\mu$; axis of nucleus, 11$\mu$.

OCCURRENCE.—This was first recorded for this region July 13, 1906, in a surface haul taken with a No. 20 net near La Jolla, California. On July 19, 1906, it was again found in a surface haul. It was frequently seen during July and August, 1917, both in the surface hauls made at the end of the pier at the

Biological Station at La Jolla and in the hauls made 4 and 6 miles offshore from 80 meters to the surface.

It was first figured by Schütt (1895) from the material of the Plankton Expedition, presumably from the Bay of Naples or the Atlantic.

SYNONYMY.—Originally figured by Schütt (1895, pl. 21, fig. 65) as *Gymnodinium spirale* var. *pinguis*, but later assigned to *Spirodinium* by Lemmermann (1899). Specific rather than varietal status for this form is indicated by its stouter fusiform shape, lack of torsion of the body, and heavy peripheral layer of rodlets, all of which characters distinguish it from *G. spirale*.

COMPARISONS.—This species is close to *G. ovoideum* in size and proportions, but is green instead of yellow and has less torsion, displacement of girdle and asymmetry.

## **Gyrodinium postmaculatum** sp. nov.

Plate 6, figure 64; plate 8, figure 91; text figure DD, 20

DIAGNOSIS.—A medium sized species with obovoidal body, its length 1.86 transdiameters; girdle a descending left spiral, displaced 0.66 transdiameter; sulcus extending from apex to antapex; surface striate with broken lines; color, amaranth purple. Length, 86$\mu$. Pacific off La Jolla, California, July, August.

DESCRIPTION.—The body is stout obovoidal to ellipsoidal in outline, rounded anteriorly, more tapering posteriorly, circular in cross-section, its length 1.86 transdiameters at the widest part, which is in the upper third of the hypocone. The hypocone exceeds the epicone in size, its length being greater by 0.09 of its own length. The epicone is elongate hemispherical anteriorly, its sides subparallel posteriorly, with the apex sometimes projecting slightly above the surrounding surface. It has a length on the left and right sides of 0.25 and 0.63 respectively of the total length of the body. The hypocone is rounded anteriorly, tapering to a slender point posteriorly. It has a length on the left and right sides of 0.7 and 0.36 respectively of the total length of the body. Its transdiameter anteriorly is greater than that of the epicone and its sides are more convex, and the antapex may be metabolic. It often forms a more or less acute antapical point.

The girdle is premedian for most of its course. Its proximal end joins the sulcus at a distance from the apex of 0.25 and its distal end 0.63 respectively of the total length of the body. Its course about the body for the first 0.5 of its length is in a nearly transverse direction, beyond which it turns posteriorly at a gradually steepening angle which becomes about 40° with the longitudinal plane of the body, at its junction with the girdle, with a displacement of 0.66 transdiameter. The furrow is narrow, having a width of about 0.02 transdiameter, and is deeply impressed with smoothly rounded edges. The sulcus reaches the apex where it forms a slightly enlarged, rounded pit, with its proximal border slightly raised above the surrounding surface. It extends posteriorly as a deep trough in a nearly straight line to within a short distance of the antapex, where it fades out. Its width is variable, narrowed anteriorly, enlarging at the anterior pore to about twice the width of the girdle, and becoming narrower again beyond the posterior pore. The anterior flagellar pore opens at the proximal junction of the girdle and sulcus, the posterior pore a short distance beyond the distal junction.

The nucleus is a large, spheroidal body filled with coarse, moniliform chromatin strands. It is slightly premedian in position, lying dorsad to the anterior flagellar pore. Its axis is about 0.52 transdiameter in length.

A large, sacklike pusule opens into the anterior flagellar pore and another, slightly smaller, into the posterior pore. The cytoplasm is finely granular and alveolate in structure and often contains one or more food masses. The body sometimes contains numerous large vacuoles filled with a fluid, colored pink like that in the pusules. Scattered profusely in its surface are minute green circles which seen in side view are the ends of small, slender, blue-green rodlets or rhabdosomes, arranged at right angles to the surface in a peripheral zone. The color of the body is amaranth purple condensed in a thin layer immediately beneath the periplast (pl. 8, fig. 91). This same coloring matter is generally collected in a denser mass at the antapex. The color may vary to something nearer a rosy tint as in figure 64, plate 6. The surface is striated with broken lines showing an amaranth purple color. On the epicone the striae are about $2.5\mu$ distant from each other at the girdle and on the proximal part of the hypocone about half that width, thus making the number on the hypocone nearly twice that on the epicone. There are about 20 across the ventral face on the epicone.

DIMENSIONS.—Length, $52–86\mu$; transdiameter, $30–45\mu$; transdiameter of nucleus, $16–22\mu$.

OCCURRENCE.—This was first taken July 9, 1904, with a No. 12 silk net, in a surface haul, 7 miles off Point Loma, California. It was taken again July 18, 1917, with a No. 25 silk net, in a surface haul, 4 miles off La Jolla, California, in a surface temperature of 20·2 C. It occurred also on July 20 and 23 in hauls made 6 miles off La Jolla from 20 and 80 meters to the surface respectively and in surface temperatures of 21°5 C and 20°8 C.

COMPARISONS.—This species, with its peripheral zone of rodlets, resembles *G. fissum* (fig. DD, 8) and *G. obtusum* (fig. DD, 3). In its coloring of amaranth purple it is unlike any other species of *Gyrodinium*, its nearest approximation being found in *Pouchetia purpurata* (pl. 8, fig. 87). The localization of the color in the peripheral layer is similar to the condition in *Pouchetia voracis* (pl. 8, fig. 89). As in many other species of the Gymnodiniidae, the colored pigment shows here also a strong tendency to collect at the apices. The localization of the pigment in the antapex, the interrupted striae, and the size are quite similar to these features in *G. rubricaudatum* sp. nov. (fig. DD, 18), but the more rotund body and the purple instead of red color differentiate the two.

## **Gyrodinium pusillum** (Schilling)

Text figure CC, 3

*Gymnodinium pusillum* Schilling (1891*a*), p. 60, pl. 3, fig. 15; (1891*b*), p. 201; *Spirodinium pusillum*, (1913), pp. 21–27, fig. 22.

*G. pusillum*, Mez (1898), p. 216.

*G. pusillum*, Schönichen and Kalberlah (1900), p. 231; (1909), p. 252.

*G. pusillum*, Massart (1901), p. 82.

*G. pusillum*, Ohno (1911), p. 91.

DIAGNOSIS.—A minute species with obliquely asymmetrical ellipsoidal body, its length 1.5 transdiameters; epicone obliquely sloped to the right; girdle a descending left spiral, displaced about 0.3 transdiameter; sulcus extending from girdle to antapex; yellow chromatophores. Length, $23\mu$. Fresh-water swamps near Basel, Switzerland.

DESCRIPTION.—The body is asymmetrical ellipsoidal, broadest in the middle and rounded at the apices, its length 1.5 transdiameters at the widest part. The hypocone exceeds the epicone in size, its length being greater by 0.22. The epicone is broad and rounded with a length on the left and right sides of 0.19 and 0.53 of the total length of the body. It slopes obliquely to the right. The hypocone is rounded on the right side with the antapex and left side sloping obliquely towards the girdle on the left side.

The girdle begins near the anterior end of the body at a distance from the apex of 0.19 of the total length of the body. It follows a descending left spiral course around the body, displaced posteriorly on the right side about 0.3 transdiameter. The furrow is wide, about 0.18 transdiameter, and is deeply impressed with overhanging borders. The sulcus extends from the girdle to the posterior end, but is omitted from Schilling's (1891*a*, 1913) figures. The transverse flagellum traverses the entire length of the girdle. The longitudinal flagellum arises near the distal end of the girdle.

Nucleus and pusules are not figured for this species. The peripheral zone of cytoplasm is filled with large, round, disklike, light yellow chromatophores. A carmine-colored stigma is present in the sulcal region below the insertion of the longitudinal flagellum.

DIMENSIONS.—Length, 23$\mu$; transdiameter, 18.4$\mu$ is given by Schilling (1891*a*) in the text, but his figures have a width of about 15$\mu$. This dimension has been used in the above description.

OCCURRENCE.—Figured by Schilling (1891*a*) from the swamps in the neighborhood of Basel, Switzerland. The only other record of its occurrence is that by Massart (1901) in brackish ditches around Palingbrug, Belgium.

SYNONYMY.—Originally described by Schilling as *Gymnodinium pusillum* and later transferred by Lemmermann (1899, 1903) to *Spirodinium*, an allocation followed by Schilling in his monograph of German fresh-water dinoflagellates (1913).

COMPARISONS.—This species, with *G. hyalinum*, are the only representatives of *Gyrodinium* thus far described from fresh water. It is also one of the four species of the genus with chromatophores. It greatly resembles *G. hyalinum*, differing from it mainly in the possession of chromatophores.

## **Gyrodinium rubricaudatum** sp. nov.

Plate 10, figure 116; text figure DD, 18

DIAGNOSIS.—A medium sized species with symmetrically ellipsoidal to biconical body, its length 2.16 transdiameters, girdle submedian, a descending left spiral displaced 0.44 transdiameter; sulcus extends from near apex to near antapex; surface with broken striae; color, greenish yellow with coral-red pigment. Length, 93$\mu$. Pacific off La Jolla, California, July, August.

DESCRIPTION.—The body is symmetrically ellipsoidal, approaching biconical, in outline, circular in cross-section, tapering towards both apices, its length 2.16 transdiameters at the widest part. The hypocone is slightly larger than the epicone in size, its length being greater by 0.08 of its own length. The epicone is convex-conical (50°) in outline with narrow, blunt apex. It has a length on the left and right sides of 0.36 and 0.58 respectively of the total length of the body. The hypocone has a slightly greater transdiameter and its sides are more convex than those of the epicone. The posterior end is prolonged into a short club-shaped projection at the antapex. The length of the hypocone on the left and right sides is about 0.62 and 0.45 respectively of the total length of the body.

The girdle is slightly premedian in position, its proximal end joining the sulcus at a distance from the apex of 0.36 and its distal end 0.56 of the total length of the body. It sweeps around the body in a nearly transverse direction for 1.5 transdiameters before it is deflected posteriorly at an angle of about 35° with the transverse plane, meeting the girdle with a displacement of 0.44 transdiameter. The furrow is rather narrow, its width being about 0.04 transdiameter, it is deeply impressed with the concavity undercutting the anterior lip and gradually curving out at the posterior one. The sulcus begins near the apex and passes posteriorly in a sinuous line to near the antapex. Its width is slightly greater than that of the girdle and it is relatively deep, fading out near both apices. The anterior flagellar pore opens in the sulcus just anterior to its proximal junction with the girdle, the posterior pore at the posterior junction.

The nucleus is a rather large ellipsoidal body, located anterocentrally. Moniliform chromatin strands follow diagonally across its longer axis. Its major and minor axes are 0.7 and 0.2 transdiameter in length respectively.

The cytoplasm is finely granular, clear and transparent, greenish yellow in color, and usually free from cell inclusions, such as food bodies. The surface is striate with blue-green striae of short dashes arranged in linear series. There are about twice as many of these on the hypocone as on the epicone, where there are about 24 across the ventral face. Our figure (DD, 18) inadequately portrays this contrast. At the antapex is a mass of coral-red pigment occupying the club-shaped projection of the body and extending more or less into the lower part of the hypocone.

DIMENSIONS.—Length, 93μ; transdiameter, 43μ; axes of nucleus, 28μ and 22μ.

OCCURRENCE.—This was taken July 17, 1906, with a No. 8 silk net, in a surface haul 1.5 miles off La Jolla, California, in a surface temperature of 21.9 C. It was quite abundant in the hauls made between July 27 and August 21, 1917, in both surface and deeper hauls. The number of individuals noted in a short examination ranged from one to seventeen in a single catch.

COMPARISONS.—This species affords the most striking example of the antapical location of its pigment, the entire amount present in the body being here concentrated in the antapex. The more common condition among the pigmented species of *Gyrodinium* is the presence of pigment in the anterior part of the body, with a scant amount, if any, in the antapical region, as in *G. maculatum* (pl. 6, fig. 62). In *G. postmaculatum* (pl. 6, fig. 64) an intermediate condition is shown, with a localized antapical pigment mass and also pigment diffused throughout the periphery. *G. rubricaudatum* leads onwards to the greater development of the same tendency in *Pavillardia* (pl. 10, fig. 114), where there is localization of the pigment in the mobile posterior tentacle.

## **Gyrodinium schuetti** Lemmermann

Text figure DD, 5

*Gymnodinium cornutum* Schütt (1895), p. 113, pl. 22, fig. 71.
*Spirodinium schuetti,* Lemmermann (1899), p. 359.

DIAGNOSIS.—A large species with broadly ellipsoidal body, its length 1.95 transdiameters; girdle a descending left spiral, displaced 0.83 transdiameter; sulcus extending from near apex to antapex; surface finely striate. Length, 117μ. Atlantic (?) or Bay of Naples.

Description.—The body is broadly ellipsoidal with broad apices, circular in cross-section, its length 1.95 transdiameters at the widest part. The epicone and hypocone are subequal in size. The epicone is elongate hemispherical in shape with broad, symmetrically rounded apex. It has a length on the left and right sides of the body of 0.42 and 0.67 respectively of the total length of the body. The hypocone in Schütt's figures presents a metabolic appearance posteriorly. This is probably due to the recent ejection of a food mass, as we have frequently observed the same appearance in *Gymnodinium heterostriatum* following the ejection of a food body when first placed under a cover slip under the microscope. In a short time the thus modified posterior part resumes its normal rounded appearance.

The girdle is a descending left spiral with a distance from the apex at its proximal and distal ends of 0.42 and 0.67 respectively of the total length of the body. The furrow has a width of about 0.06 transdiameter, becoming narrower at its distal end, and is rather shallow, with smooth, overhanging borders. The sulcus extends from the apex to the antapex in a slightly sinuous line. The transverse flagellum arises at the proximal junction of the girdle and sulcus, the longitudinal flagellum midway between the distal junction and the antapex.

The nucleus is a large ellipsoidal body, filled with parallel moniliform chromatin strands, and lying in the anterocentral part of the body, oblique to the longitudinal axis. Its major and minor axes are about 0.73 and 0.48 transdiameter in length respectively. The anterior end of the body is filled with large alveoli. The surface of the body is closely beset with longitudinal, beaded striae, nearly equal in number on both epicone and hypocone, about 30 across the ventral face. Color (?).

Dimensions.—Length, 117μ; transdiameter, 60μ; axes of nucleus, 44μ and 29μ.

Occurrence.—Figured by Schütt (1895) presumably from material of the Plankton Expedition from the Atlantic or from the Bay of Naples.

Synonymy.—This organism was described by Schütt as *Gymnodinium cornutum* n. sp., a name which was preoccupied by Pouchet (1885*a*) in his *G. cornutum* (=*Gyrodinium cornutum* (Pouchet) Kofoid and Swezy); it was later changed by Lemmermann (1899) to *Spirodinium schuetti*.

Comparisons.—The only other species of *Gyrodinium* with striae and a rotund epicone are *G. truncus* sp. nov., *G. grave* (Meunier), *G. pingue* (Schütt), *G. maculatum* sp. nov., and *G. postmaculatum* sp. nov. (figs. DD, 4, 7, 15, 19, 20). *G. truncus* is more rotund, with shorter epicone and fewer striae; *G. grave* is a smaller species with much more displacement and torsion of girdle; *G. pingue* is a smaller species with more slender body and relatively greater displacement; *G. maculatum* is much smaller, is pigmented, and has more intercingular torsion; and *G. postmaculatum* has a pointed pigmented antapex.

### **Gyrodinium spirale** (Bergh)

Plate 4, figure 43; text figure DD, 14

*Gymnodinium spirale* Bergh (1881*a*), p. 66; (1881*b*), pp. 253–255, pl. 16, figs. 70, 71.
*G. spirale*, Saville-Kent (1880–1882), p. 858.
*G. spirale*, Pouchet (1883), pp. 446, 447; (1885*a*), pp. 44, 67–69, pl. 4, fig. 30.
*G. spirale*, Daday (1884), p. 13, fig. 4.
*G. spirale*, Klebs (1884), p. 730; (1912), pp. 429, 430.
*Spirodinium spirale*, Entz, Sr. (1884), p. 39; Entz, Jr. (1902*a*), p. 92; (1902*b*), p. 119; (1905), p. 108; (1907), pp. 17, 24; (1909), pp. 254, 255.
*Gymnodinium spirale*, Bütschli (1885), pp. 965, 974, 975, 993, 1017, 1018, pl. 51, fig. 5.

*G. spirale*, Schilling (1891), pp. 200, 205, 206.
*G. spirale*, Whitelegge (1891), pp. 181, 188, pl. 28, fig. 8.
*G. spirale*, Schütt (1895), pp. 35, 37, 95, 113, 117; as *Spirodinium spirale* (1896), p. 5, fig. 6.
*G. spirale*, Delage and Hèrouard (1896), p. 384, fig. 666.
*G. spirale*, Jörgensen (1899), p. 26.
*Spirodinium spirale*, Lemmermann (1899), p. 339; (1901), p. 358; (1902), p. 260.
*S. spirale*, Schröder (1900), p. 13; (1911), pp. 620, 626, 651.
*S. spirale*, Pavillard (1905), p. 47.
*Gymnodinium spirale*, Dogiel (1906), pp. 40, 41, 43.
*G. spirale*, Karsten (1907), p. 335.
*Spirodinium spirale*, Paulsen (1907), p. 24; (1908), pp. 101, 102, fig. 140.
*Gymnodinium spirale*, Francé (1908), p. 48.
*G. spirale*, Doflein (1909), p. 461, fig. 412; (1911), p. 527, fig. $472_3$.
*G. spirale*, Herdman (1911*b*), p. 72; (1911*c*), p. 40.
*Spirodinium spirale*, Schiller (1912), p. 28.
*S. spirale*, Cavers (1913), pp. 182, 183, fig. $9_{14}$.
*S. spirale*, Ostenfeld (1913), pp. 123, 338, 344, 476.
*S. spirale*, West (1916), p. 51, fig. 36*c*.
*S. spirale*, Lebour (1917*b*), p. 193, fig. 10*a*.

Diagnosis.—A medium sized species with fusiform body, its length 2.5 transdiameters; girdle a descending left spiral, displaced 1.19 transdiameters; sulcus extending from apex to antapex; surface striate; color, ivory yellow. Length, 105μ to 150μ. Cosmopolitan marine habitat.

Description.—The body is slender fusiform, widest posteriorly, tapering anteriorly, nearly circular in cross-section, its length 2.5 transdiameters at the widest part. The dorsal side is convex, the ventral subconcave, giving both apices a slight ventrad deflection and the whole body a small degree of asymmetry, which is most noticeable in lateral view. The greatest length of the hypocone is somewhat less than that of the epicone, but its size is greater, due to its continuously greater transdiameter. The epicone has the shape of a cone of about 40°, convex on the left and dorsal sides and becoming concave on the right and ventral sides. The apex is blunt. It has a length on the left and right sides of 0.3 and 0.76 respectively of the total length of the body. The sides of the hypocone are subparallel anteriorly, rounded posteriorly, deeply notched on the left side of the antapex by the distal end of the sulcus, with the right side forming a rounded lobe extending 0.19 transdiameter beyond the left.

The girdle is a steeply descending left spiral with a displacement of 1.19 transdiameters or 0.47 of the total length of the body. Its proximal end joins the sulcus at a distance from the apex of 0.3 and its distal end 0.76 of the total length of the body, with an overhang of about 0.19 transdiameter. The furrow has a width of about 0.08 transdiameter and is deeply impressed with smooth borders which are generally undercut and somewhat elevated above the surrounding surface. The sulcus extends from the apex to the antapex with a torsion of about 0.19 transdiameter. Its width is about half that of the girdle in the intercingular area, narrower anteriorly and widening somewhat posteriorly where it excavates the left side of the antapex. The anterior flagellar pore opens at the proximal junction of the girdle and sulcus, the posterior pore about one width of the girdle below the distal junction.

The nucleus is ellipsoidal to spheroidal in shape and is situated in the anterocentral part of the body. It is filled with fine moniliform, subparallel chromatin strands. Its major and minor axes are about 0.47 to 0.71 (to 0.56 transdiameter in the spheroidal form) in length.

Small sacklike pusules may be present at either pore or at both. In the individual figured the posterior pusule was very large and the anterior one absent. The cytoplasm is very finely

granular, clear and transparent, and often contains large vacuoles and food masses, evidences of a holozoic mode of nutrition. The surface is beset with equidistant, longitudinal, blue-green striae which are about twice as numerous on the hypocone as on the epicone, which has about 15 across the ventral face. The general color of the organism varies from pale, glaucous green to ivory yellow.

DIMENSIONS.—Length, 105–150$\mu$; transdiameter, 40–45$\mu$; axes of nucleus, 20$\mu$ and 30$\mu$ to 24$\mu$ and 24$\mu$.

OCCURRENCE.—Our first record for this species is June 3, 1907, 2.25 miles off La Jolla, California, in a haul from 120 meters to the surface. On July 18, 1917, it was found in a surface haul at the end of the pier at the Biological Station and on July 20 in a haul 6 miles offshore from 80 meters to the surface and a surface temperature of 21° C.

It was first figured by Bergh (1881) from the Baltic Sea. Other records of its occurrence are as follows: Pouchet (1883–1885*a*) in the Atlantic off Concarneau, France, in October; Entz, Jr. (1902) in the Adriatic Sea; Whitelegge (1891), Port Jackson, Sydney, Australia, in April and May; Jörgensen (1899), in the Atlantic off Puddefjord, and Hardangerfjord, Norway, in April and July; Schröder (1900) in the Gulf of Naples (1911) and Adriatic Sea, in July; Pavillard (1905) in the Gulf of Lyons in October; Karsten (1907) in the Indian Ocean, 1° 40.′6 S, 41° 47.′1 E, in March; Herdman (1911) at Port Erin, Isle of Man; Ostenfeld (1913) in Baltic Sea off coast of Denmark, July, August; and Lebour (1917*b*) at Plymouth Sound, England.

SYNONYMY.—This species was originally described by Bergh (1881) as *Gymnodinium spirale* and later utilized by Schütt (1896) as the type species of his genus *Spirodinium*. Pouchet (1883) has characterized five varieties of this species, of which he names only two, *G. spirale* var. *nobilis* and *G. spirale* var. *striatum*. The characters given to these are such that it is not possible to reidentify them. His variety *D* is probably *Gymnodinium heterostriatum*.

COMPARISONS.—This is the type species of the genus *Gyrodinium*, following Schütt's use of it as his type species in his genus *Spirodinium*, which it replaces. It also is the type of the subgenus *Gyrodinium*. In the torsion and shape of the body it resembles *G. biconicum*, but is distinct from it in the presence of surface striae. In the overhang of the girdle and the slight amount of torsion in the intercingular sulcus it looks forward to the next genus, *Cochlodinium*.

Our figures show a stouter body with less contraction at the apices than do Bergh's (1881*b*); but our material includes forms as slender as he has figured, though these are less typical of the species as we find it.

### **Gyrodinium spumantia** sp. nov.

Plate 7, figure 72; text figure CC, 13

DIAGNOSIS.—A large species with irregularly obovoidal body, its length 1.8 transdiameters; girdle a descending left spiral, displaced 0.43 transdiameters; sulcus extends from apex to antapex; color, pink, grey and yellow ochre. Length, 146$\mu$. Pacific off La Jolla, California, August.

DESCRIPTION.—The body is irregular, asymmetrical obovoidal in outline, its broadest transdiameter premedian, its length 1.8 transdiameter at the widest part, which is at the girdle. The entire outline of the body is uneven and ridged, but without wrinkling of the pellicle resulting from shrinkage. The size of the hypocone is somewhat greater than that of the epicone, its length being greater by 0.13 of its own length. The shape of the epicone is roughly conical (50°) with irregular metabolic sides. It has a length on the left and right sides of 0.32 and 0.56 respectively of the total length of the body. The apex is blunt and notched by the sulcus. The hypocone is somewhat narrower (35°) than the epicone, also irregular in outline, with a more slender, pointed antapex. Its length on the left and right sides is about 0.65 and 0.43 respectively of the total length of the body.

The girdle is premedian for the greater part of its length. Its proximal end joins the sulcus at a distance from the apex of 0.32 and its distal end 0.56 of the total length of the body. The first 0.5 transdiameter of its course follows a nearly transverse direction around the body, beyond which it is deflected posteriorly in an increasingly steeper angle, its distal end being displaced about 0.43 transdiameter. The furrow is narrow, its width being about 0.03 transdiameter, and is deeply impressed with overhanging borders.

The sulcus extends from the apex to the antapex as a shallow, narrow trough. Its direction is that of a sigmoid curve anteriorly, less sinuous posteriorly. The anterior flagellar pore opens at the proximal junction of the girdle and sulcus, the posterior pore midway between the distal junction and the antapex.

The nucleus is spheroidal and situated in the right central part of the body. It is filled with coarse chromatin strands. Its axis is about 0.3 transdiameter in length.

A small sacklike pusule opens into each flagellar pore. The cytoplasm presented a foamy appearance with finely granular constituency and was completely filled with large vacuoles containing a pink fluid, with blue-green droplets and dark, refractive granules. These were so massed together as to give the body a dense appearance and without sharp contrast in its various parts. The basal color of the cytoplasm is pearl grey with minute dots of yellow ochre which become dense in the girdle region, the anterior part of the sulcus and at the antapex. A thick cluster of melanin granules was present in the apical region on the right side of the sulcus. There were no striations or other surface markings.

DIMENSIONS.—Length, 146$\mu$; transdiameter, 81$\mu$; axis of nucleus, 26$\mu$.

OCCURRENCE.—A single individual was taken August 21, 1917, with a No. 25 silk net, 5 miles off La Jolla, California, in a haul from 83 meters to the surface.

COMPARISONS.—In the foamlike structure of its cytoplasm, which may, however, be only a transient metabolic condition, this species resembles *G. flavidum* (pl. 7, fig. 73) and *Gymnodinium multistriatum* (pl. 4, fig. 37), without the firm pellicle of the latter species. It is the only species in the genus showing the presence of melanin which is common in the more highly specialized genera, *Pouchetia* and *Erythropsis*. This may have come from ingested food. Its labile body is unique in *Gyrodinium*.

## **Gyrodinium submarinum** sp. nov.

Plate 10, figure 110; text figure DD, 1

DIAGNOSIS.—A large species with slender fusiform body, its length 3.54 transdiameters; girdle a descending left spiral, displaced 1.75 transdiameters; sulcus extending from apex to antapex; surface striate; color, dull glaucous blue. Length, 117$\mu$. Pacific off La Jolla, California, July.

Description.—The body is long, slender fusiform, circular in cross-section, tapering towards both ends, but slightly truncate posteriorly, its length 3.54 transdiameters at the widest part, which is near the middle. The epicone and hypocone are subequal, though the posteriorly extending point on the right ventral side gives to the epicone a slightly greater length. The epicone is convex conical (45°) anteriorly with a pointed apex, but posteriorly its sides are subparallel with only a slight convexity. It has a length on the left and right sides of 0.27 and 0.76 respectively of the total length of the body. The hypocone is convex conical with a greater transdiameter posteriorly than the corresponding part of the epicone, with the antapex obliquely truncate on the right side of the sulcal notch. Its sides are slightly more convex than those of the epicone.

The girdle is a steeply descending left spiral, its proximal end joining the sulcus at a distance from the apex of 0.27 and its distal end 0.76 of the total length of the body, giving it a displacement of 1.75 transdiameters or about 0.5 of the total length of the body. The furrow has a width of about 0.07 transdiameter and is deeply impressed on its anterior side, where it undercuts the lip, becoming more shallow towards its posterior border. Both lips are smooth and somewhat protuberant. The sulcus extends from the extreme anterior tip of the body posteriorly in a slightly sinuous line to the antapex. It is narrow anteriorly, widening slightly in the intercingular area and again near the posterior end of the body, where it deeply notches the right side of the antapex. Its greatest width is less than that of the girdle. The anterior flagellar pore opens at the proximal junction of the girdle and sulcus, the posterior pore immediately posterior to the distal junction.

The nucleus is long ellipsoidal to conform to the shape of the body and is filled with moniliform chromatin strands lying parallel with its long axis. It is located dorsad of the intercingular area, near the center of the body. Its major and minor axes are about 1.36 and 0.33 transdiameters in length respectively.

A small, sacklike pusule opens into the anterior flagellar pore. The cytoplasm is finely granular and transparent with numerous yellowish green spherules and oil droplets scattered through it. A large refractive body of irregular shape, outlined with a dark border, nearly filled the apical region in front of the anterior flagellar pore. The antapical region contained a group of refractive spherules closely massed together and outlined by a dark ring. The color of the body is a pale dull glaucous blue diffused through the cytoplasm. The surface is closely beset with numerous, equidistant, longitudinal, blue-green striae, the number on the hypocone slightly greater than that on the epicone, 25 to 30 across the ventral face.

Dimensions.—Length, 117μ; transdiameter, 33μ; axes of nucleus, 45μ and 11μ.

Occurrence.—Three individuals were taken July 25, 1917, with a No. 25 silk net, 5 miles off La Jolla, California, in a haul from 80 meters to the surface and in a surface temperature of 20° C.

Activities.—This is an extremely active form under the microscope, moving in large loose clockwise spirals with a slow rotation on the long axis. The spiral is occasionally reversed to the anticlockwise direction.

Comparisons.—In the slender fusiform shape of body this species resembles *G. britannia* sp. nov. (fig. DD, 13) and *G. acutum* (Schütt) (fig. CC, 7), differing from both, however, in the character of its surface markings and in the greater displacement of its girdle, and from the former species also in its lack of pigmentation. It is the most slender and one of the most active species in the genus.

## **Gyrodinium truncatum** sp. nov.

Plate 1, figure 3; text figure CC, 5

Diagnosis.—A small species with subovoidal body, its length 1.62 transdiameters; girdle submedian, a descending left spiral, displaced 0.4 transdiameter; sulcus short on epicone, extending to antapex on hypocone: color, yellow green shading to yellow ochre posteriorly. Length, 57μ. Pacific off La Jolla, California, July.

Description.—The body is broadly ovoidal or almost biconical, tapering at both ends with truncate apex, widest posterior to the middle, its length 1.62 transdiameters at the widest part, which is near the girdle. In cross-section the body is nearly circular. The epicone has a slightly greater length than the hypocone, but its actual size is about the same. It is truncate conical of about 60° in shape, contracted towards the apex, and has a length on the left and right sides respectively of about 0.38 and 0.63 of the total length of the body. The hypocone is rotund anteriorly, tapering abruptly posteriorly to an acute tip, with the left side more convex than the right. It has a length on the left and right sides of about 0.57 and 0.33 of the total length of the body.

The girdle is submedian in position, its proximal end joining the sulcus at a distance from the apex of 0.38 and its distal end 0.63 of the total length of the body. Its course around the body is that of a descending left spiral, displaced posteriorly 0.4 transdiameter. The furrow has a width of about 0.07 transdiameter and is deeply impressed, with a rounded outline, which undercuts both borders slightly. The sulcus invades the epicone for a short distance as a rather shallow trough and extends posteriorly in a slightly sinuous line which fades out near the antapex. The anterior flagellar pore is located at the proximal junction of the girdle and sulcus, the posterior pore midway of the distance between the distal junction and the antapex.

The nucleus is a reniform body filled with moniliform chromatin strands and is found in the posterior part of the body, in the region of the posterior pore, with its long axis in a transverse plane. Its major and minor axes are 0.71 and 0.31 transdiameters in length respectively.

A small sacklike pusule opens into each flagellar pore. The cytoplasm is very finely granular, clear and transparent with a few oil drops scattered through it, and contains a number of food bodies, evidence of holozoic nutrition. In the anterior portion of the body was a large food mass yellow grey in color. Near it was a smaller, greenish refractive body and in the antapical region another one, yellow ochre in color. The general color of the organism is greenish yellow, shading to yellow ochre posteriorly. A thin-walled, hyaline cyst, somewhat larger than the body, invested the organism.

Dimensions.—Length, 57μ; transdiameter, 35μ; axes of nucleus, 21μ and 11μ; length of cyst, 67μ.

Occurrence.—A single individual was taken July 11, 1917, with a No. 25 net, in a haul 4 miles off La Jolla, California, from 80 meters to the surface and in a surface temperature of 19°8 C.

Comparisons.—This is one of the species of *Gyrodinium* which shows the nearest approximation to the *Gymnodinium* type of the girdle arrangement, and is probably one of the connecting links with that genus. It is one of the more generalized species in *Gyrodinium*, and in that respect resembles *G. ovum* (Schütt) and *G. foliaceum* nom. sp. nov. (figs. CC, 8, 18), lacking, however, the chromatophores of the latter species.

## **Gyrodinium truncus** sp. nov.

Plate 3, figure 28; text figure DD, 4

DIAGNOSIS.—A large species with body rotund, subellipsoidal, its length 1.48 transdiameters; girdle a descending left spiral, displaced 0.64 transdiameters; sulcus extending from apex to antapex; surface coarsely striate; color, greenish yellow. Length, 83μ. Pacific off La Jolla, California, August.

DESCRIPTION.—The body is large, of robust habit, and asymmetrical outline, its length 1.48 transdiameters at the widest part, which is below the girdle. The posterior end is pointed and the anterior end is asymmetrical and almost truncate in outline with the girdle region on the left side forming a high shoulder. A cross-section of the body is nearly circular. The hypocone greatly exceeds the epicone in size, its length being greater by 0.39 of its own length. The epicone is somewhat excentric, the left side being raised, forming an angle of 60° with the longitudinal axis of the body and terminating in a high, shoulder-like ridge about 0.09 of the length of the body below the apex. The epicone lengthens until it reaches 0.54 of the total length of the body on the right side of the sulcus. The apex is broad and truncate in outline. The hypocone is very broad with rounded sides which contract abruptly to a point at the antapex, which is notched on the left side by the distal end of the sulcus.

The girdle is a descending left spiral, which meets the sulcus proximally about 0.09 of the total length of the body below the apex. Its distal junction with the sulcus occurs at 0.54 of the total length of the body below the apex, giving it a displacement of 0.64 transdiameters. It lies in a wide, deep depression, its width about 0.05 transdiameter, with smoothly rounded, overhanging borders, both of which are undercut by the furrow. The anterior flagellar pore is located at the anterior junction of the girdle and sulcus and the posterior pore far posterior, less than 0.2 transdiameter from the antapex. The transverse flagellum was short, traversing but a short proximal section of the girdle.

The sulcus extends from the apex to the antapex. Below the anterior flagellar pore it lies in a shallow trough with overhanging sides, the borders of which are unevenly serrate, the right border extending beyond the left in a flap which obscures the furrow.

The nucleus is large, ellipsoidal and situated slightly below the central portion of the body, with its long axis oblique to that of the body. Large, moniliform chromatin threads follow its major axis. Its major and minor axes are 0.71 and 0.5 transdiameters in length respectively.

A small sacklike pusule opens into each flagellar pore. The cytoplasm is very finely granular, and contains food bodies and other evidences of holozoic nutrition. In the individual figured two large, irregular-shaped, yellowish green and greyish green food bodies were found close beside the nucleus. In the epicone were three groups of dark, refractive oil globules. Smaller blue-green oil droplets were scattered through the anterior half of the body. The general color of the protoplasm is yellowish green in the anterior portion of the body shading to a yellow ochre and old gold in the antapical region. The surface of the body is striate with blue green, equidistant lines extending from the girdle to the apices, 15 in number across the ventral face of the epicone. These are about 7μ apart on the epicone and 4μ on the hypocone side of the girdle.

DIMENSIONS.—Length, 83μ; transdiameter, 55μ; axes of nucleus, 42μ and 27μ.

OCCURRENCE.—A single individual was taken August 17, 1917, with a No. 25 silk net, 0.75 mile off La Jolla, California, in a haul from 80 meters to the surface and in a surface temperature of 21°9 C.

COMPARISONS.—In the unusual asymmetry of the body this form closely resembles *G. flavidum* sp. nov. (fig. CC, 20), differing from it, however, both in

color and in its surface markings, the latter being entirely absent in *G. flavidum*. There is a difference between the two in their apices, which are much more developed in *G. flavidum* than in *G. truncus*.

## **Gyrodinium virgatum** sp. nov.

Plate 10, figure 112; text figure DD, 21

Diagnosis.—This is a stout medium sized species with subrhomboidal body, its length 1.45 transdiameters; girdle a descending left spiral, displaced 0.73 transdiameter; sulcus extending from apex to antapex; surface coarsely striate; color, greenish yellow with coral-red pigment. Length, 93$\mu$. Pacific off La Jolla, California, August.

Description.—The body is asymmetrical, subrhomboidal in shape, tapering conical anteriorly, its length 1.45 transdiameters at the widest part, which is at the girdle. In cross-section the body is nearly circular. The epicone and hypocone are subequal in size. In the individual figured the posterior end was truncate and drawn out to the left, as though having recently discharged a food body. A second individual showed the posterior end having a shape somewhat similar to the anterior end. The epicone is broadly conical, subtending an angle of about 80° with the right side almost twice the length of the left, and the apex narrowly rounded. The length of the epicone on the left of the sulcus is 0.21 and on the right is 0.72 of the total length of the body. The hypocone is distorted in the individual figured in that the antapex is drawn out on the left side to a broadly truncate form. A second individual in the same material showed the hypocone slightly rounder than the epicone with a broadly rounded antapex. Both epicone and hypocone form wide, flaring shelves at the girdle region.

The proximal and distal ends of the girdle join the sulcus at about 0.21 and 0.72 respectively of the total length of the body from the apex. The girdle sweeps around the body in a descending left spiral course which is displaced at the right side posteriorly 0.71 transdiameter. The furrow has a width of about 0.05 transdiameter, and is deeply impressed with broad, flaring borders raised above the surface of the body. The anterior flagellar pore is located at the proximal junction of the girdle and sulcus and the posterior pore slightly below the distal junction.

The sulcus is a wide, deep trough which extends from the apex to the antapex in an almost straight line. It varies slightly in width throughout, narrow anteriorly and wider posteriorly, with smooth rounded borders.

The nucleus is large, kidney-shaped and is located slightly below the equatorial plane. It is differentiated into two parts, an outer alveolar layer and an inner region filled with large chromatin granules without linear arrangement. The outer layer is about 0.1 of the minor axis of the nucleus in thickness and is composed of ellipsoidal, pink vacuoles arranged with their long axis perpendicular to the surface of the nucleus. The major and minor axes of the nucleus are 0.6 and 0.3 transdiameter in length respectively.

A large, sacklike pusule opens into the anterior flagellar pore. The cytoplasm is very finely granular, clear and transparent. A large pink vacuole in the antapical region and numerous dark refractive bodies were present, the products, probably, of holozoic nutrition. The general color of the cytoplasm is greenish yellow. The surface is striate with rather widely separated, equidistant, blue-green striae. These are more numerous on the hypocone, the epicone containing approximately one-half the number on the hypocone. The striae on the epicone are beset with masses of coral-red pigment and number 15 across the ventral face. The pigment may take the form of beads or long masses following the line of striae, or of irregular splashes. Several large rounded masses of coral red were located near the apex. A few granules of coral red were found on the hypocone.

DIMENSIONS.—Length, 79–90$\mu$; transdiameter, 52–68$\mu$; axes of nucleus, 84$\mu$ and 48$\mu$.

OCCURRENCE.—Two individuals were taken August 8, 1917, with a No. 25 net, 4 miles off La Jolla, California, in a haul from 80 meters to the surface and in a surface temperature of 21°9 C.

ACTIVITIES.—The movements of this organism were rather sluggish, showing a slow clockwise rotation. It invariably came to rest with the ventral face on the substrate.

COMPARISONS.—The relative proportions and size of this species alone separate it from *G. corallinum* (fig. DD, 12). The type of nucleus is peculiar and constant in all of the individuals of both species that were observed. A similar structure is found in *Gymnodinium rubrum* (pl. 8, fig. 86). It is unlike anything found elsewhere in the Gymnodinioidae.

One might be inclined to regard this species as an aberrant form of *G. corallinum* were it not for the fact that several individuals referable to it, of apparently normal status, have been encountered. In addition the relative degree of displacement of the girdle, with reference to the transdiameter, separates it from that species, as does also the location of the posterior pore. The marked differences in the shape of the nuclei in the two species may be due to approaching mitosis in the individual of *G. virgatum* which we figure, and not to a fundamental specific difference.

## **Gyrodinium viridescens** sp. nov.

Plate 4, figure 48; text figure DD, 11

DIAGNOSIS.—A small species with broadly subfusiform body, concave posteroventrally, dorsoventrally flattened, its length 1.95 transdiameters; girdle displaced one transdiameter; sulcus encircling an apical lobe and reaching the antapex; surface striate; color, pale pea green; littoral habitat. Length, 45$\mu$. Sandy beach of the Pacific at La Jolla, California, July.

DESCRIPTION.—The body is broadly subfusiform, asymmetrical, tapering anteriorly, obliquely truncate posteriorly, its length 1.95 transdiameters. Its greatest transdiameter is near the middle of the hypocone, slightly anterior to the middle of the body. The dorsoventral diameter is 0.66 of the transverse one. The epicone forms less than 0.3 of the total body, its altitude at the proximal and distal ends of the girdle being respectively 0.13 and 0.61 of the total length of the body. Owing to the rapid descent of the distal end of the girdle the right ventral lobe of the epicone is projected posteriorly as a slender triangular process. The apex is a rounded cone higher than a hemisphere and somewhat more rotund on the left face and bears a central lobe or button about 0.2 transdiameter across, encircled by the anterior end of the sulcus. The hypocone forms more than 0.7 of the whole body, and is higher and more convex on the left than on the right side. From the midventral level posteriorly the whole ventral face is flattened and somewhat concave centrally, to such an extent that the posterior margin lies dorsal to the major axis. The antapex is obliquely truncate for a width of 0.5 transdiameter and slopes from the left posteriorly to the right at an angle of 10° from the horizontal.

The girdle starts far anterior, within 0.13 of the total length of the body from the anterior end, ascends about 0.5 furrow's width in its proximal quarter, then descends in an ever steeper spiral across the back and down the ventral face to its junction with the sulcus at about 0.61 of the total length of the body from the apex. The total displacement is one transdiameter at the widest part of the body, or 0.5 the total length. The furrow is about 0.11 of a transdiameter in width, nearly uniform to the distal end where it narrows slightly, and is not deeply impressed. The transverse flagellum nearly encircles the body. The sulcus runs the whole length of the body, passing anteriorly upon the epicone and almost completely encircling a central terminal field as a slightly elevated button. It is very narrow and shallow in this region. It forms a flat sigmoid curve on the ventral face and flares below the posterior flagellar pore located below the junction of the distal end of the girdle, in a wide excavation 0.5 transdiameter in width across the antapex. There is no flap over the sulcus and the right posterior margin is the longer, a distinction generally attained by the left side in most asymmetrical dinoflagellates. The posterior flagellum extends beyond the antapex for a distance of 0.7 the total length.

The surface is finely and uniformly striate with equidistant longitudinal lines of equal numbers on epicone and hypocone. There are about 18 across the ventral face. The nucleus is ellipsoidal, located slightly anterior to the middle with its major axis inclined a little to the right. Its length is about 0.6 transdiameter. Numerous small greenish bodies of varying sizes and subspheroidal shape of a high refractive index fill the cytoplasm. They appear to be reserve food of a fatty nature. Near the posterior end is a small ellipsoidal body of yellow ochre color, either a chromatophore or a small ingested food body. The general color is a suffused pale pea green without localized chromatophores.

Dimensions.—Total length, 40–46$\mu$; transdiameter at widest part, 22$\mu$; dorsoventral diameter, 16$\mu$; length of nucleus, 16$\mu$.

Occurrence.—Rare in the beach sands off La Jolla, California, in July, 1914.

Comparisons.—This species differs from all other species thus far described in the genus (including all species in the old genus *Spirodinium* Schütt) in that it has the well defined loop of the sulcus around an apical button, as in some forms of *Cochlodinium*. The posteroventral excavation is also unusually extensive. The fine striation on the surface is a common feature in many species, though the uniformity on epicone and hypocone is not so generally present. It is most like *Gyrodinium herbaceum* sp. nov. and *G. pingue* (Schütt) (figs. DD, 6, 15) in general form, displacement of girdle, asymmetry and tendency to truncate form of the antapex. It is, however, much smaller, 45$\mu$ instead of 70$\mu$ in length, has the apical loop of the sulcus which Schütt (1895) does not figure, and has the girdle more anteriorly located as a whole. It also lacks the rhabdosomes or rodlets which appear to characterize Schütt's species. In its dorsoventral flattening, green color, and small epicone it approaches the species of *Amphidinium* with which it is associated in the beach sands. It is the only known arenaciphilous member of the genus *Gyrodinium*.

CHAPTER XIV

# GYMNODINIIDAE: COCHLODINIUM

## **COCHLODINIUM** Schütt

Text figures O, FF–HH

*Gymnodinium,* Schütt (1895), in part, pl. 22, fig. 72; pl. 23, figs. 75, 76; pl. 24, fig. 77; pl. 26, fig. 93.

*Cochlodinium* Schütt (1896), pp. 5, 6, figs. 1, 7.

*Cochlodinium,* Paulsen (1908), in part, pp. 103–105, figs. 142–145 (fig. 144 = *Gyrodinium longum*).

### Diagnosis

Gymnodiniidae with torsion of the body of at least 1.5 turns; girdle a descending left spiral of 1.5 or more turns, widely displaced; sulcus with or without apical and antapical loops and a torsion of 0.5 or more turns. Nucleus usually in center or posterior part of body, rarely anterior; perinuclear membrane generally absent; moniliform chromatin strands distinct. Pusules usually present, opening anteriorly into the anterior flagellar pore, posteriorly into the posterior pore, frequently united at their extremities into one canal opening into both pores. No nematocysts; plasma varying from colorless to highly colored; chromatophores rarely present; holozoic nutrition prevalent; melanin or other pigment granules sometimes present. Surface may be smooth or, less frequently, striate. Encystment in thin-walled membrane frequent. Rarely a tendency to colonial formation. Length, 27–200μ. All marine, eupelagic and from warm temperate seas. Thirty species known.

### Organology

In the elongation of the girdle and sulcus and the torsion of the body resulting therefrom the genus *Cochlodinium* shows the greatest development in the Gymnodinioidae, or indeed in the Dinoflagellata. The length of the girdle (fig. FF, *gir.*) is intimately correlated with the torsion and constriction of the body in *Cochlodinium*, differing in this respect from the genus *Pouchetia*, where the length, course, and torsion of the sulcus are the outstanding features of its organization. The greater development of the apical and antapical loops of the sulcus so striking in *Pouchetia* is foreshadowed in *Cochlodinium* in *C. clarrissimum* (fig. GG, 2), *C. miniatum* (fig. GG, 6), and *C. atromaculatum* (fig. HH, 6).

In the simpler, more generalized species of *Cochlodinium* we find a type of girdle only slightly removed from that of *Gyrodinium*, as in *C. scintillans* (fig. GG, 11), where the girdle is 1.5 turns in length, with a torsion of 0.5 in the sulcus. The greatest development of the girdle is found in *C. augustum* (fig. HH, 15), and *C. pulchellum* (fig. HH, 16), the former with four turns, the latter with nearly three turns around the body, with a corresponding development of the sulcus. Intermediate stages between these two extremes are common.

The torsion of the body, as shown in the sulcus, is confined almost exclusively to the intercingular region with, rarely, an apical or antapical loop added thereto. The striking exceptions are *C. clarissimum* and *C. atromaculatum*, the former with an apical, the latter with an antapical loop. In this respect the genus differs from *Pouchetia*, where the apical or antapical regions may show as much if not more torsion than the intercingular area.

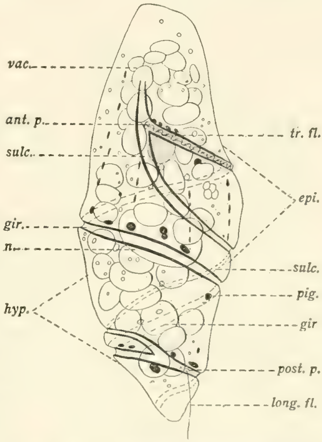


Fig. FF. *Cochlodinium atromaculatum* sp. nov. Abbreviations: *ant. p.*, anterior flagellar pore; *epi.*, epicone; *gir.*, girdle; *hyp.*, hypocone; *long. fl.*, longitudinal flagellum; *n.*, nucleus; *pig.*, pigment; *post. p.*, posterior pore; *sulc.*, sulcus; *tr. fl.*, transverse flagellum; *vac.*, vacuoles. × 500.

With the lengthening of the girdle and the resulting torsion of the body a profound change takes place in the orientation of the organism. Considering the longitudinal plane passing through the flagellar pores as the dorsoventral plane of the body, the two pores both open on the ventral face, as in *Amphidinium*, *Gymnodinium*, and nearly all the species of *Gyrodinium*. With the lengthening of the girdle in some species of *Gyrodinium* and in *Cochlodinium* the posterior pore is pushed around the body and, while the median longitudinal plane lies midway between them, the morphological median dorsoventral plane undergoes torsion with the body. Thus in all the simpler species of *Cochlodinium* the anterior pore opens on the right, the posterior pore on the left face of the figure, as in *C. vinctum* (fig. HH, 3). The posterior pore may thus be carried completely around the body and regain its position in the same median plane with the anterior pore, as in *C. radiatum* (fig. GG, 12) with two turns of the girdle and in *C. augustum* (fig. HH, 15) with four turns of the girdle. This position, however, in which both pores come to lie together in the median plane, is secondarily acquired, and the morphological dorsoventral plane has undergone a torsion of two or four full turns respectively to accomplish the results.

The constriction of the body is closely correlated with the length of the girdle and sulcus. In forms with the shorter girdle, as 1.5 turns in *C. cavatum* (fig. HH, 10), the body is nearly always greatly constricted on the morphologically ventral face, with a resulting ventral excavation of the body, as in *C. cavatum* and *C. helix* (fig. HH, 8), or with the ventral surface thrown into rounded lobes, as in *C. vinctum* (fig. HH, 3) and *C. conspiratum* (fig. GG, 10), with the dorsal side convex in both cases. The most aberrant form in this respect is *C. distortum* (fig. HH, 9). With the lengthening of the girdle the constrictions extend around the body, as in *C. lebourae* (fig. HH, 7), the number of lobes increasing with the turns of the girdle and sulcus until the maximum in the genus is reached in *C. augustum* (fig. HH, 15).

The borders of the sulcus are not protuberant, yet they are apparently capable of great distension, as the sulcal area evidently forms the region for the ingestion of food. Comparatively huge food bodies are frequently noted in the cytoplasm, as in *C. rosaceum* (pl. 8, fig. 85), and the ingestion of these must place great strain on the sulcal region, particularly in forms like *C. augustum*.

The nucleus is usually located near the posterocentral part of the body. Its chromatin contents are always arranged in the beaded, moniliform threads characteristic of the Dinoflagellata generally. Two species only, *C. miniatum* (fig. GG, 6) and *C. strangulatum* Schütt, present a perinuclear membrane of the type occasionally found in *Gyrodinium*.

The cytoplasmic organization in the genus *Cochlodinium* never reaches the relatively high degree of differentiation sometimes found in *Gymnodinium* and *Gyrodinium*. The nearest approach to ectoplasmic differentiation is seen in *C. clarissimum* (pl. 5, fig. 60), with its superficial vacuolated layer. The peripheral zone of short rodlets so prominent in *Gyrodinium* is rarely met with in this genus, *C. citron* alone presenting it (fig. HH, 12).

The surface of the body in this genus is relatively free from striae, and, unlike the genus *Pouchetia*, striae are here associated with primitive or more generalized species with one exception, *C. distortum* (fig. HH, 9). Only three other species have striae, *C. volutum* (fig. GG, 1), *C. pirum* (fig. GG, 3), and *C. mineatum* (fig. GG, 6).

The color of the cytoplasm in the genus *Cochlodinium* is varied, often brilliant and changeable in tone. The color may be diffused throughout, as in *C. rosaceum* (pl. 8, fig. 85), *C. citron* (pl. 7, fig. 79), and *C. conspiratum* (pl. 3, fig. 29), or it may be massed in clumps or irregular bodies. In *C. radiatum* (pl. 6, fig. 67) the aster-purple pigment is found in irregular, leaflike masses scattered through the periphery. The yellow ochre of *C. atromaculatum* (pl. 7, fig. 71) is scattered through the peripheral zone while the melanin is aggregated into ellipsoidal masses along the girdle.

In *C. distortum* (pl. 7, fig. 78) the ochraceous-orange color is distributed along the surface striae in globules of varying sizes, recalling similar conditions

in *Gyrodinium,* as in *G. maculatum* (pl. 6, fig. 62). One species, *Cochlodinium geminatum* (fig. HH, 1), contains yellow-ochre chromatophores.

Nearly all the colors of the spectrum are to be found within this genus, with a preponderance of yellow and yellow ochre. At the red end of the spectrum are *C. archimedes, C. constrictum, C. rosaceum* (pl. 8, fig. 85), and *C. miniatum* (pl. 10, fig. 107), with aster purple in *C. radiatum* (pl. 6, fig. 67). A faint reddish tone is found in *C. scintillans* (pl. 10, fig. 113) and *C. augustum* (pl. 5, fig. 53). Three species are green in color, *C. convolutum* (pl. 10, fig. 115), *C. faurei* (pl. 2, fig. 25), and *C. clarissimum* (pl. 5, fig. 60), the latter obscured by pink peripheral vacuoles. Two species have a bluish tint, *C. vinctum* (pl. 2, fig. 15) and *C. pulchellum* (pl. 2, fig. 21), and the remainder are yellow and yellow ochre in color, varying in a few species to a yellow green.

All the species in the genus *Cochlodinium* are probably holozoic in nutrition, with the possible exception of the one species containing chromatophores, *C. geminatum.* In the other species, with few exceptions, the cytoplasm contains evidences of holozoic nutrition in the form of food masses, refractive rodlets, vacuoles and oil globules, the accumulated products of metabolism. There is some slight evidence in *C. vinctum* (fig. HH, 3) of selective feeding.

Cyst formation is common throughout the genus, the cyst consisting of a thin-walled hyaline membrane. Occasionally double cysts are formed, one within the other. In some species binary fission takes place within the cyst, as in *C. pulchellum* (figs. HH, 14, 16). In other cases cyst formation is evidently correlated with the ingestion of food balls and serves as a digestion cyst, as in *C. clarissimum* (fig. GG, 2) and *C. cavatum* (fig. HH, 10).

## Distribution

The genus *Cochlodinium* as a whole is somewhat more restricted in its range than either *Gymnodinium* or *Gyrodinium.* It has no fresh-water representatives. All the species thus far described have come from warm temperate waters, with none from the polar or tropical seas. Possible exceptions to this may be found in the species described by Schütt (1895), since he unfortunately omitted to mention the localities from which his species were obtained. They were presumably from the Bay of Naples or the warm Atlantic from the collection of the Plankton Expedition, and make up half the number of the previously described species. His species are *C. constrictum, C. geminatum, C. pirum, C. schuetti* (= *Gymnodinium helix*, Schütt, 1895, in part), and *C. strangulatum.* Two more species described by Pouchet (1883, 1887) complete the record for the Atlantic. These are *C. archimedes* and *C. helix. C. pirum* has also been recorded from the Mediterranean at Naples, Italy, by Entz, Jr. (1909).

The only *Cochlodinium* thus far recorded from the Baltic is *C. pellicidum*, near Kiel, Germany, by Lohmann (1908). A single species has been figured from Yokohama Harbor, Japan, *C. catenatum*, by Okamura (1916). Three species have been recorded from Plymouth Sound, England, by Miss Lebour (1917*b*).

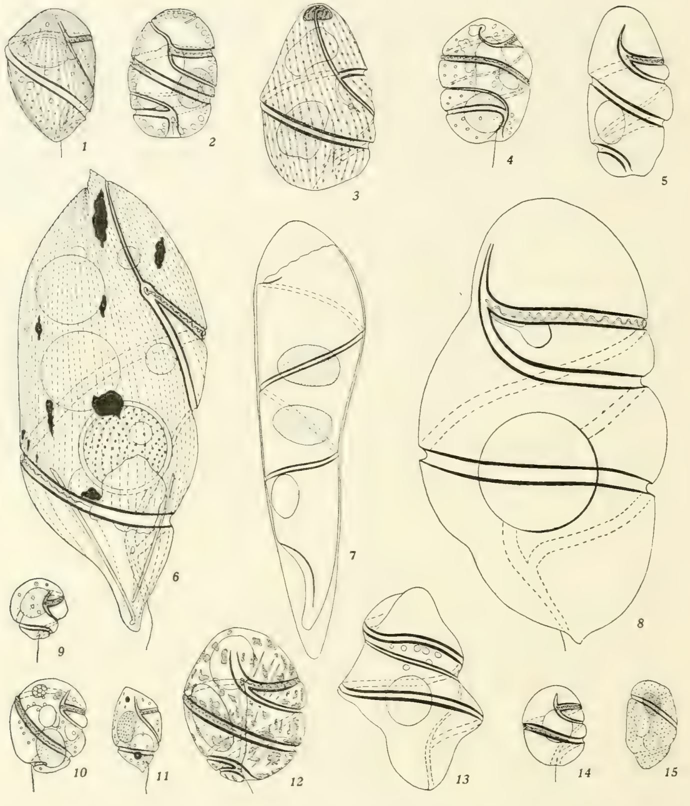

Fig. GG. *Cochlodinium.* 1. *C. volutum* sp. nov. 2. *C. clarissimum* sp. nov. 3. *C. pirum* (Schütt) Lemm. After Schütt (1895, pl. 23, fig. $76_1$). 4. *C. faurei* sp. nov. 5. *C. cereum* sp. nov. 6. *C. miniatum* sp. nov. 7. *C. elongatum* sp. nov. 8. *C. strangulatum* Schütt. After Schütt (1895, pl. 22, fig. $72_1$). 9. *C. turbineum* sp. nov. 10. *C. conspiratum* sp. nov. 11. *C. scintillans* sp. nov. 12. *C. radiatum* sp. nov. 13. *C. constrictum* (Schütt) Lemm. Modified after Schütt (1895, pl. 26, fig. 93). 14. *C. catenatum* Okamura. 15. *C. pellucidum* Lohmann. After Lohmann (1908, pl. 17, fig. 21). × 500.

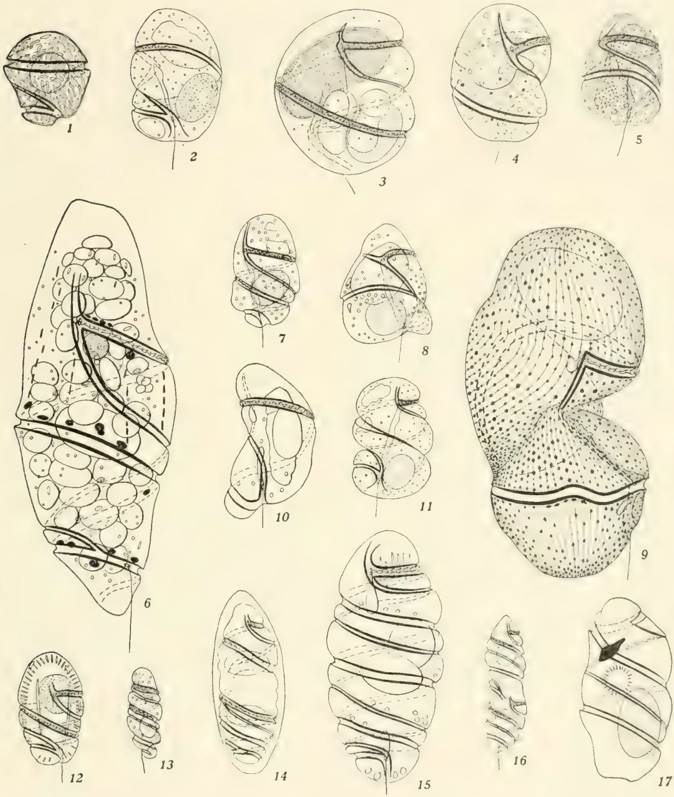


Fig. HH. *Cochlodinium.* Magnification 500, except where otherwise stated. 1. *C. geminatum* (Schütt) Lemm. After Schütt (1895, pl. 23, fig. $75_2$, lower figure). 2. *C. schuetti* sp. nov. 3. *C. vinctum* sp. nov. 4. *C. rosaceum* sp. nov. 5. *C. convolutum* sp. nov. 6 *C. atromaculatum* sp. nov. 7. *C. lebourae* sp. nov. 8. *C. helix* (Pouchet) Lemm. 9. *C. distortum* sp. nov. 10. *C. cavatum* sp. nov. 11. *C. virescens* sp. nov. 12. *C. citron* sp. nov. 13. *C. pulchellum* Lebour. 14. *C. pulchellum* Lebour. × 625. Early stage of division. 15. *C. augustum* sp. nov. 16. *C. pulchellum* Lebour. Late stage of division. 17. *C. archimedes* (Pouchet) Lemm. After Pouchet (1883, fig. M).

To the single record made by Okamura for the Pacific we add in this paper from the plankton off San Diego and La Jolla, California, the following species previously described: *C. catenatum* Okamura, *C. helix* (Pouchet), *C. pulchellum* Lebour, *C. pirum* (Schütt); and the following twenty-one new species: *C. atromaculatum, C. augustum, C. cavatum, C. cereum, C. citron, C. clarissimum, C. conspiratum, C. convolutum, C. distortum, C. elongatum, C. faurei, C. lebourae, C. miniatum, C. radiatum, C. rosaceum, C. schuetti, C. scintillans, C. turbineum, C. vinctum, C. virescens,* and *C. volutum.*

The most widely distributed species is *C. pirum*, recorded from the Mediterranean, the Atlantic, and the Pacific.

## Historical Discussion

The genus *Cochlodinium* was established by Schütt (1896) for the forms previously described as *Gymnodinium* without ocellus in which the girdle had a length of 1.5 turns or more. His type species was *C. strangulatum* (= *Gymnodinium strangulatum* Schütt (1895). He did not follow this up by sifting out these species from *Gymnodinium*, and that was later done by Lemmermann (1899) as follows:

*Gymnodinium archimedes* Pouchet (1883) = *Cochlodinium archimedes* (Pouchet) Lemm.
*Gymnodinium helix* Pouchet (1887) = *Cochlodinium helix* (Pouchet) Lemm.
*Gymnodinium constrictum* Schütt (1895) = *Cochlodinium constrictum* (Schütt) Lemm.
*Gymnodinium pirum* Schütt (1895) = *Cochlodinium pirum* (Schütt) Lemm.
*Gymnodinium geminatum* Schütt (1895) = *Cochlodinium geminatum* (Schütt) Lemm.

In 1908 Lohmann added to the list of species in *Cochlodinium* two species, *C. pellucidum* and *C. longum*. The latter form has a girdle which seems to make one turn only about the body, hence we regard it as a *Gyrodinium*, and have tentatively placed it in that genus as *G. longum*.

Okamura (1916) added one species to the genus, *C. catenatum*, and Lebour in 1917 described *C. pulchellum*, bringing the total number of valid species in the genus up to nine: *C. archimedes* (Pouchet) Lemm., *C. catenatum* Okamura, *C. constrictum* (Schütt) Lemm., *C. geminatum* (Schütt) Lemm., *C. helix* (Pouchet) Lemm., *C. pellucidum* Lohmann, *C. pirum* (Schütt) Lemm., *C. pulchellum* Lebour, and *C. strangulatum* Schütt. To these we add herewith twenty-one new species from the plankton of the Pacific off La Jolla, California: *C. atromaculatum, C. augustum, C. cavatum, C. cereum, C. citron, C. clarissimum, C. conspiratum, C. convolutum, C. distortum, C. elongatum, C. faurei, C. lebourae, C. miniatum, C. radiatum, C. rosaceum, C. scintillans, C. schuetti, C. turbineum, C. vinctum, C. virescens,* and *C. volutum.*

## Subgenera of Cochlodinium

### Subgenus 1. **Cochlodinium** subgen. nov.

Body not excavated sinistroventrally, girdle of 1.5 to 2, rarely 2.5, turns. Type species *Cochlodinium strangulatum* Schütt.

This subgenus includes all the species which do not show special differentiation in the form of the body or the extreme amount of torsion, the greatest amount being that indicated by two (or at the most 2.5 turns) turns of the girdle. It is consequently the largest subgenus in number of species. These fall naturally into three groups according to the amount of torsion of the body. The first group, which we term the *C. miniatum* group, has a torsion of the body as shown in the girdle of 1.5 turns. It includes *C. miniatum* sp. nov., *C. scintillans* sp. nov., *C. turbineum* sp. nov., *C. catenatum* Okamura, *C. volutum* sp. nov., and *C. pirum* (Schütt). This group as a whole lies near the borderline separating this genus from *Gyrodinium*. It also contains the only species with striate surface, a striking *Gyrodinium* characteristic.

The second group, the *Cochlodinium strangulatum* group, has a torsion of about 1.7 turns of the girdle. It contains *C. strangulatum* Schütt, *C. constrictum* (Schütt), *C. pellucidum* Lohmann, *C. conspiratum* sp. nov., and *C. cereum* sp. nov.

The third group, the *C. citron* group, has a torsion of the body as indicated by about 2 turns of the girdle. It includes *C. citron* sp. nov., *C. lebourae* sp. nov., *C. faurei* sp. nov., *C. clarissimum* sp. nov., *C. archimedes* (Pouchet), *C. virescens* sp. nov., *C. radiatum* sp. nov., *C. atromaculatum* sp. nov., and probably *C. elongatum* sp. nov.

### Subgenus 2. **Glyphodinium** subgen. nov.

Body asymmetrical, excavated sinistroventrally, arched dextrodorsally, more or less deeply incised by the sulcus, girdle of 1.5 to 1.6 turns. Type species, *Cochlodinium cavatum* sp. nov.

This subgenus includes a small group of species with asymmetrical, more or less excavated and constricted body. It includes *Cochlodinium geminatum* (Schütt), *C. schuetti* sp. nov., *C. rosaceum* sp. nov., *C. vinctum* sp. nov., *C. convolutum* sp. nov., *C. helix* (Pouchet), *C. cavatum* sp. nov., and *C. distortum* sp. nov. These species form an orthogenetic series of increasing curvature and distortion, culminating in the huge, much distorted and highly colored *C. distortum*.

### Subgenus 3. **Polydinium** subgen. nov.

Body elongate, fusiform, its length more than 2 transdiameters, girdle a descending left spiral of more than 3 turns, sulcus with more than 2 turns. Type species *Cochlodinium augustum* sp. nov.

This subgenus includes only those species with the extreme amount of torsion of the body, as indicated by three or more turns of the girdle. It includes in consequence the most highly differentiated species, in this particular, in the genus. As might be expected, the number of species therein is small. It contains only two species, *Cochlodinium augustum*, the type, and *C. pulchellum* Lebour.

## Key to the Species of **Cochlodinium**

1. Girdle with 1.5–2.5 turns ........ 2
1. Girdle with 3–4 turns (subgenus **Polydinium**) ........ 28
2. Two sides of body symmetrical, girdle with 1.5–2.5 turns (subgenus **Cochlodinium**) ........ 3
2. Two sides of body markedly asymmetrical, girdle with 3–4 turns (subgenus **Glyphodinium**) ........ 21
3. Girdle with about 1.5 turns ........ 4
3. Girdle with about 1.7 turns ........ 9
3. Girdle with about 2–2.5 turns ........ 13
4. Surface not striate ........ 5
4. Surface striate ........ 7
5. Color reddish-grey, body biconical ........ **scintillans** sp. nov.
5. Color green to yellow ........ 6
6. Body obovoidal, narrower posteriorly, green ........ **turbineum** sp. nov.
6. Body ellipsoidal, greenish yellow ........ **catenatum** Okamura
7. Length 200$\mu$, with coral-red pigment ........ **miniatum** sp. nov.
7. Length less than 100$\mu$, no red pigment ........ 8
8. Epicone smaller than hypocone, green ........ **volutum** sp. nov.
8. Epicone and hypocone subequal, yellow ochre ........ **pirum** (Schütt)
9. Large species, 198$\mu$, perinuclear zone present ........ **strangulatum** Schütt
9. Smaller species, less than 100$\mu$, no perinuclear zone ........ 10
10. Cytoplasm colorless, body subellipsoidal, 39$\mu$ ........ **pellucidum** Lohmann
10. Color present ........ 11
11. Girdle salient, body rose color, 90$\mu$ ........ **constrictum** (Schütt)
11. Girdle not salient, body yellow ........ 12
12. Length 1.2 transdiameters, 40$\mu$ ........ **conspiratum** sp. nov.
12. Length 2 transdiameters, 76$\mu$ ........ **cereum** sp. nov.
13. Girdle with 2.5 turns, rose color ........ **archimedes** (Pouchet) Lemm.
13. Girdle with less than 2.5 turns, not reddish ........ 14
14. Large species, exceeding 100$\mu$ ........ 15
14. Smaller species, less than 100$\mu$ ........ 16
15. Body fusiform, 184$\mu$, ochraceous with melanin ........ **atromaculatum** sp. nov.
15. Body club-shaped, larger anteriorly, 174$\mu$, opaline green ........ **elongatum** sp. nov.
16. Color bluish with aster-purple splotches, body broadly ellipsoidal ........ **radiatum** sp. nov.
16. Color green to yellow ........ 17
17. Color yellow to yellowish green ........ 18
17. Color green ........ 19
18. Color amber yellow, not deeply constricted, radial rhabdosomes ........ **citron** sp. nov.
18. Color yellowish green, deeply constricted by sulcus and girdle ........ **virescens** sp. nov.
19. Length 1.66 transdiameters, antapex contracted, lumiere green ........ **lebourae** sp. nov.
20. Length 1.36 transdiameters, greenish grey ........ **faurei** sp. nov.
20. Length 1.50 transdiameters, glaucous green ........ **clarissimum** sp. nov.
21. With vermiculate yellow ochre chromatophores, body contracted posteriorly ........ **geminatum** (Schütt)
21. No chromatophores, antapex rotund except in **cavatum** ........ 22

22. Body striate, orange yellow, labile, deeply constricted ............ **distortum** sp. nov.
22. No striae ............ 23
23. Rose color ............ **rosaceum** sp. nov.
23. Blue, yellow, or green ............ 24
24. Right lobe of antapex protuberant ............ 25
24. Antapex symmetrical, rotund ............ 26
25. Ventral surface arched, 66$\mu$, oil yellow ............ **cavatum** sp. nov.
25. Not arched ventrally, 54$\mu$, yellowish green ............ **helix** (Pouchet) Lemm.
26. Displacement of girdle .82 transdiameter, green ............ **convolutum** sp. nov.
26. Displacement less than .82 transdiameter ............ 27
27. Antapex very rotund, glaucous blue with yellow tinge ............ **vinctum** sp. nov.
27. Antapex flattened, pale yellowish green ............ **schuetti** sp. nov.
28. Girdle with 3 turns, 40$\mu$ ............ **pulchellum** Lebour
28. Girdle with 4 turns, 111$\mu$ ............ **augustum** sp. nov.

## **Cochlodinium archimedes** (Pouchet) Lemm.

Text figure HH, 17

*Gymnodinium archimedes* Pouchet (1883), pp. 51, 52, fig. M; (1885*a*), pp. 52, 53, pl. 4, fig. 41; (1885*b*), pp. 529, 530; (1887), pp. 94, 95.
*G. archimedes,* Bütschli (1885), pp. 922, 924, 964, 965, 986, pl. 51, fig. 9.
*G. archimedes,* Schütt (1895), p. 36.
*Cochlodinium archimedes,* Lemmermann (1899), p. 360.
*C. archimedes,* Paulsen (1908), pp. 103, 104, fig. 142.

Diagnosis.—A medium sized species with asymmetrical, ellipsoidal body, its length 2.05 transdiameters; girdle a descending left spiral of 2.5 turns, displaced 1.45 transdiameters; sulcus with torsion of at least 1.5 turns; color, rose. Length, 76$\mu$. Concarneau, France.

Description.—The body is ellipsoidal, somewhat constricted by the furrows; asymmetrically rounded anteriorly, obliquely truncate posteriorly, its length 2.05 transdiameters at the widest part near the middle. The epicone and hypocone are subequal in length, but the hypocone is slightly greater in size. The epicone is small and button-like anterior to the proximal part of the girdle. It has a length from the proximal and distal ends of the girdle of 0.13 and 0.85 respectively of the total length of the body. Its distal portion is a broad band, tapering distally and making 1.5 turns around the body. The distal portion of the hypocone is convex ventrally, concave dorsally, and obliquely truncate posteriorly.

The girdle joins the proximal end of the sulcus about 0.1 of the total length of the body from the apex. It sweeps around the body in a descending left spiral course forming an angle of about 30° to 35° with the longitudinal axis of the body. It passes around the body with 2.5 turns and meets the distal end of the sulcus about 0.15 of the total length of the body from the antapex. It is relatively wide and deeply impressed. The positions of the flagellar pores were not recorded by Pouchet.

The sulcus follows the course of the girdle in its posterior descent of 1.5 turns around the body. It is shallow with a width about half that of the girdle, and terminates at its junction with the girdle posteriorly. The anterior invasion of the epicone is not figured, but the probability of such an extension occurring is suggested by the notch on the dorsal side of the apex, which in other species is usually made by the anterior end of the sulcus. The indentation at the posterior end of the body also suggests its extension in that direction.

The nucleus is ellipsoidal and is situated in the anterior part of the body. Its chromatin contents are arranged in strands following its longer axis. Its major and minor axes are about 0.57 and 0.45 transdiameter.

Near the center of the body is a sphere formed by short rodlets radially arranged. This probably corresponds to the large spherical masses with radially arranged rodlets such as are figured in *Gymnodinium dogieli* sp. nov. (pl. 3, fig. 34) and *G. radiatum* sp. nov. (text fig. Z, 9). In the anterior part of the body is an irregular scarlet-pigment mass, which may probably be the remains of a food body. This has been described by Paulsen (1908) as a stigma. It may be, however, only a colored food mass such as may be seen occasionally in other species of the Gymnodinioidae, as *Gymnodinium aureum* (pl. 1, fig. 5), *Gyrodinium melo* (pl. 5, 50), and many others.

Occurrence.—Figured by Pouchet (1883, 1885*a*) from the Atlantic off Concarneau, France, in July.

Synonymy.—This was originally described by Pouchet (1883, 1885*a*) as a species of *Gymnodinium*, and was transferred to *Cochlodinium* by Lemmermann (1899). In the form which Pouchet described in 1883 the girdle makes two turns around the body, both ends terminating on the same face, resulting in an entirely different dorsoventral orientation of the body. In his later figure (1885*a*) the girdle makes 2.5 turns with the ends terminating on opposite faces of the body. This, if valid, would place them in different species, but Pouchet states in his later paper that the figure given therewith is a more correct representation than his earlier figure.

Comparisons.—Only two species in the genus, *C. augustum* (fig. HH, 15) and *C. pulchellum* (fig. HH, 16), have a greater torsion of the body than *C. archimedes*, the first having a girdle of four turns, the second of three turns. It is placed in the *C. citron* group of the subgenus *Cochlodinium*, leading towards the subgenus *Polydinium*.

### **Cochlodinium atromaculatum** sp. nov.

Plate 7, figure 71; text figures FF; HH, 6

Diagnosis.—A large species with elongate ellipsoidal body, its length 2.7 transdiameters; girdle a descending left spiral of 2 turns, displaced 1.5 transdiameters; sulcus with antapical loop, torsion of 1.7 turns; melanin present; color, grey and ochraceous orange. Length, 184μ. Pacific off La Jolla, California, July.

Description.—The body is elongate ellipsoidal or asymmetrical subfusiform, obliquely truncate anteriorly, tapering posteriorly and circular in cross-section, its length 2.7 transdiameters at the widest part at the middle. The epicone exceeds the hypocone in size. It is relatively long anterior to the anterior pore with nearly straight sides and obliquely truncate apex. Its length at the proximal and distal ends of the girdle is 0.28 and 0.82 respectively of the total length of the body. Posterior to the proximal junction of the girdle and sulcus it becomes contracted to a slender band which makes one complete turn around the body, ending in a slender point at the distal junction. The hypocone sweeps around the body in a broad band from three to six times the width of the posterior part of the epicone, making one complete turn above the distal junction of the girdle and sulcus. Posteriorly it forms a cone of about 65° with rounded antapex.

The girdle meets the sulcus at a distance from the apex at its proximal and distal ends of 0.28 and 0.82 respectively of the total length of the body. It sweeps around the body at an angle of about 30° with the transverse plane, forming a descending left spiral of two turns, joining the sulcus at a distance from the antapex of 0.16 of the total length of the body with a displacement of 1.5 transdiameters. The furrow has a width of about 0.08 transdiameter and is deeply impressed, undercutting the anterior border and curving gradually to the posterior one. The borders are smooth and rounded. The sulcus invades the epicone for a short distance anterior to its proximal junction with the sulcus. It sweeps posteriorly in a descending left spiral which forms an angle of about 50° with the transverse plane in the first part of its course, gradually changing in the latter part of its course to about 30°. The furrow is about half the width of the girdle for the first half of its length, becoming narrower distally and enlarging again posterior to the distal junction with the girdle. It is deeply impressed with rounded sides. Posterior to the distal junction it makes a loop of nearly 0.6 turn, terminating at the right side of the antapex on the dorsal side of the body. The anterior flagellar pore is located at the anterior junction of the girdle and sulcus, the posterior pore a short distance beyond the distal junction on the same side of the body.

The nucleus is an ellipsoidal body posterocentrally located, its long axis slightly oblique to the transverse plane of the body. Its major and minor axes are 0.64 and 0.35 transdiameter in length respectively.

Pusules were not present in the individual figured. The cytoplasm is coarsely granular and is nearly filled with large ellipsoidal and spheroidal bodies and vacuoles of a clear, pale grey color. Near the equatorial region were some smaller green oil globules and scattered over the surface were minute blue-green droplets and mingled with them short green rodlets. In addition a large, rounded, ochraceous-orange food mass was located near the anterior pore. Its cytoplasmic inclusions are evidences of a holozoic mode of nutrition. The color has for its background a pearl grey which is almost clear at the apex and elsewhere is thickly beset with minute ochraceous-orange granules, or dots. These last are numerous near the surface and at the antapex. Along the margin of the girdle and sulcus are large pigment masses varying in size and black in color. From the middle region of the body a few rows, four to a semicircle, of small rod-shaped melanin granules extend to the girdle at the left of the sulcus, and at the right of it to nearly midway between the anterior pore and the apex. No striae or other surface markings could be detected, though the linear arrangement of the small melanin granules suggests a fundamental linear organization of the superficial cytoplasm.

Dimensions.—Length, 183–185$\mu$; transdiameter, 72$\mu$; axes of nucleus, 45$\mu$ and 23$\mu$; length of longitudinal flagellum, 45$\mu$. The figure given of this species (pl. 7, fig. 71) is the only one in our plates which shows the longitudinal flagellum in any species with its full length.

Occurrence.—Two individuals were taken on July 20, 1917, with a No. 25 silk net 6 miles off La Jolla, California, in a haul from 80 meters to the surface and in a surface temperature of 20°5 C.

Comparisons.—This is one of the largest species of the genus *Cochlodinium*, being exceeded in size only by *C. strangulatum* (fig. GG, 8) with a length of 210$\mu$. It is the only species in the genus showing the presence of melanin and the second species in all of the genera below *Pouchetia*, the other being *Gyrodinium spumantia* (pl. 7, fig. 72).

*C. atromaculatum* belongs in the *citron* group of the subgenus *Cochlodinium*, and differs from the remainder of the group mainly in the greater elongation of the body and in the presence of an antapical loop, the latter feature foreshadowing the condition in the higher genus *Pouchetia*.

ACTIVITIES.—This is an active organism, moving in loose circles in an anti-clockwise direction with rotation on its major axis in a clockwise directon, reversing occasionally.

### **Cochlodinium augustum** sp. nov.

Plate 5, figure 53; text figure HH, 15

DIAGNOSIS.—A large species with fusiform body, its length 2.3 transdiameters; girdle a descending left spiral of 4.1 turns, displaced 0.74 total length; sulcus with short apical loop, torsion 3.1 turns; color, greenish grey with a tinge of salmon pink; holozoic. Length, 108μ. Pacific off La Jolla, California, August.

DESCRIPTION.—The body is symmetrically fusiform, elongated, deeply constricted by girdle and furrow, its length 2.3 transdiameters at the equator. The epicone very slightly exceeds the hypocone in size. Its length at the proximal and distal ends of the girdle is 0.14 and 0.88 respectively of the total length of the body. The apex is asymmetrically rounded, deflected to the left and only slightly grooved on the ventral surface by the shallow ascending loop of the sulcus. The hypocone has a length of 0.86 and 0.12 respectively of the total length at the proximal and distal ends of the girdle. The antapex is flattened hemispherical in form, furrowed ventrally by the distal end of the sulcus, but is without a sulcal notch in the postmargin.

The girdle leaves the sulcus 0.14 of the total length of the body from the apex. It sweeps around the body in a descending left spiral of 4.1 turns before joining the sulcus distally at a point distant from the antapex 0.12 of the total length of the body. It forms a fairly uniform spiral deflected 20° from the horizontal except at the two ends where it is flattened almost to the horizontal. It lies in a deep depression throughout its course and has high overarching borders. The lips are smooth, with a green line along its anterior side. Its width is 0.09 transdiameter. The anterior flagellar pore is located at the anterior junction and the posterior flagellar pore at the posterior junction of the girdle and sulcus. The transverse flagellum was very short in the individual figured, traversing scarcely 0.5 turn of the girdle. The longitudinal flagellum is about half the length of the body in length.

The sulcus invades the hypocone a short distance, forming a shallow, slightly curved loop terminating near the apex. Below the pore it follows the course of the girdle midway between its turns, reaching the posterior junction of the two after 3.1 turns. It lies in a narrow deep depression and is a slender trough 0.5 the width of the girdle. Beyond the pore it traverses the hypocone vertically for a short distance as a deep trough terminating near the antapex without sulcal notch.

The nucleus is an ellipsoidal body centrally located, its major axis nearly coinciding with the short axis of the body. Chromatin threads could not be found in its very transparent substance. Its major and minor axes are 0.5 and 0.3 transdiameter respectively in length.

A large club-shaped pusule opens anteriorly into the anterior flagellar pore and a slightly smaller one posteriorly into the posterior pore. The cytoplasm is granular. A few small blue-green oil globules were present, one group in the anterior part of the body and another group below the midregion, all near the girdle. In addition there were three groups of pink vacuoles in the peripheral plasm, two along the left margin and a third of four much larger, ellipsoidal vacuoles near the antapex. One large, spheroidal, greenish food mass was located near the nucleus. Near the apex is a group of slender, sharp-pointed, greenish rhabdosomes or rodlets arranged longitudinally near the proximal end of the girdle at the left of the main axis. The color is a mixture of grey, blue green, and salmon pink, the last strongest around the border of the body. No surface markings or striations were observed.

DIMENSIONS.—Length, 108μ; transdiameter at the widest part of the body, 47μ; axes of nucleus, 25μ and 16μ.

OCCURRENCE.—Two individuals were taken August 13, 1917, with a No. 25 silk net in a haul 0.75 mile off La Jolla, California, from 83 meters to the surface, in a surface temperature of 21°9 C.

COMPARISONS.—There are only four species of this genus larger than *C. augustum*, to wit: *C. atromaculatum*, 184μ; *C. distortum*, 156μ; *C. miniatum*, 200μ; and *C. strangulatum*, 200μ. This species has more torsion than any known member of the Gymnodinioidae, or of the Dinoflagellata as a whole. The nearest to it is in *C. pulchellum* Lebour (fig. HH, 16) with a torsion of its sulcus of 2.25 turns to the 3.1 turns of *C. augustum*. It is the most specialized member of the subgenus *Polydinium* and one of the most differentiated in *Cochlodinium* also. Its specialization is also indicated by its large size. The nine different channels which cross the "ventral" face of this organism are so close to each other and divide up the surface so completely that there must be considerable stretching and distension of adjacent regions wherever the animal feeds on an object as large as the food ball figured in our specimen.

## **Cochlodinium catenatum** Okamura

Plate 9, figure 105; text figure GG, 14

*Cochlodinium catenatum* Okamura (1916), p. 41, figs. 1–3.

DIAGNOSIS.—A minute species with rotund ellipsoidal body, its length 1.29 transdiameters; girdle a descending left spiral of 1.5 turns, displaced 0.7 transdiameters; sulcus with torsion of 0.5 turn; color, light yellowish green to yellow ochre; tending to form colonies. Length, 35μ. Pacific off La Jolla, California, July, August; Yokohama Harbor, Japan, June.

DESCRIPTION.—The body is rotund ellipsoidal with broad, rounded apices, nearly circular in cross-section, its length 1.29 transdiameters at the widest part, which is at the middle. The epicone and hypocone are subequal in size. The epicone is subhemispherical anteriorly with broad symmetrically rounded apex. It has a length from the proximal and distal ends of the girdle of 0.25 and 0.80 respectively of the total length of the body. The hypocone is also subhemispherical in shape with broad antapex slightly notched by the distal end of the sulcus.

The girdle is a descending left spiral of 1.5 turns, distant from the apex at its proximal and distal ends about 0.25 and 0.8 respectively of the total length of the body, with a displacement of 0.7 transdiameter. The furrow has a width of about 0.07 transdiameter and is deeply impressed with smooth, rounded sides. The sulcus invades the epicone to near the apex as a slender trough which fades out anteriorly. Posteriorly it is deflected to the left below the proximal junction with the girdle, with a torsion of 0.5 turn in the intercingular area before meeting the distal end of the sulcus, beyond which it takes a nearly straight course to the antapex. The anterior flagellar pore opens at the proximal junction of the girdle and sulcus, the posterior pore at the distal angle of the posterior junction.

The nucleus is spheroidal and is located near the center of the body. Its axis is about 0.5 transdiameter in length.

The cytoplasm is finely granular, clear and transparent, and contained no vacuoles or other cell inclusions in the individuals examined, while another contained a small, partly digested

*Gymnodinium,* and a few slender, blue green rodlets. Nutrition is holozoic. The color is a diffuse light yellowish green. No striae or other markings could be detected on its surface. In figure 105, plate 9, a chain of four zooids is figured. These are the products of recent mitoses, which have not yet separated.

DIMENSIONS.—Length, 35µ; transdiameter, 28–35µ; axis of nucleus, 14–16µ.

OCCURRENCE.—This was first seen July 12, 1917, when a single individual and a chain of four zooids were taken with a No. 25 net in a haul 6 miles off La Jolla, California, from 80 meters to the surface and in a surface temperature of 20°6 C. On July 18 it was again present in a haul 4 miles offshore, in a haul from 80 meters to the surface and a surface temperature of 20°8 C.

Okamura (1916) described this species from the waters of Yokohama Harbor, Japan, in June, 1910 and 1911, at which time it occurred so abundantly that the waters were discolored a dark reddish brown and fish were found floating on the surface in a dying condition.

SYNONYMY.—Okamura has described minute linear or dotlike chromatophores, yellowish brown in color, in the forms he observed. These were not present in the individuals found at La Jolla and may possibly have been food bodies or oil droplets. The two forms correspond so closely in other respects that it seems inadvisable to separate them.

COMPARISONS.—Chain formation as a result of rapid schizogony is not uncommon in the Dinoflagellata; it may be temporary or permanent, and may occur in both the naked and thecate forms. Many species of *Gonyaulax* and *Ceratium* form temporary chains. One species of *Gonyaulax* (Kofoid and Rigden, 1912) and the two species of the genus *Polykrikos* form permanent colonies. In Okamura's material single individuals of *Cochlodinium catenatum* were rare, chains of 4, 8, 16, and intermediate numbers being common, showing a strong tendency towards permanency or true colony formation.

This species belongs to the *C. miniatum* group of the subgenus *Cochlodinium*. It is the smallest symmetrically ellipsoidal species in the genus, with the minimum amount of torsion, and represents the most primitive condition in *Cochlodinium* in structure.

### **Cochlodinium cavatum** sp. nov.

Plate 9, figure 93; text figure HH, 10

DIAGNOSIS.—A medium sized species with body asymmetrically reniform, excavated ventrally, arched dorsally, with a right antapical lobe; length 2.25 transdiameters; girdle a descending left spiral of 1.5 turns, displaced 0.64 total length; sulcus with apical and antapical loops, and a torsion of 0.5 turns, plasma oil yellow. Length, 66µ. Pacific off La Jolla, California, July.

DESCRIPTION.—The body is elongated, markedly concave on the ventral face and convex on the dorsal, thus throwing both apices excentrically ventrad. This gives to the body a twisted reniform shape. The epicone exceeds the hypocone in length by 0.14 of the total length of the

body. The epicone has a length on the left of 0.23 and on the right of the sulcus of 0.87 of the total length of the body. It is in lateral view a conoid of 35° with hemispherical apex. The greatest length of the hypocone is 0.77 of the total length of the body, while at the right of the sulcus its length is only 0.13 of the total length. The antapical region is markedly asymmetrical, the right side projecting as a hemispherical lobe 0.5 transdiameter in diameter.

The girdle joins the proximal end of the sulcus 0.23 of the total length of the body from the apex. It sweeps around the body in a descending left spiral course. In the proximal 0.5 turn it is deflected posteriorly only about 15°, but in the next 0.5 it turns posteriorly in a sigmoid curve deflected 45° to 60°, until it reaches a point 0.03 of the total length of the body from the antapex, where it slackens again to 25° for a short distance and joins the distal end of the sulcus. It is relatively wide, 0.14 transdiameter, and is deeply impressed with smooth overhanging borders. The anterior flagellar pore opens at the anterior junction of the girdle and sulcus, the posterior pore, 0.5 transdiameter above their distal junction.

The sulcus invades the epicone as a longitudinal groove which terminates near the apex. As a descending left spiral it makes 0.5 turn before meeting the distal end of the girdle 0.13 of the total length of the body from the antapex, where it forms a deep, wide excavation on the face of the hypocone. It is a narrow, rather shallow groove with smooth borders lying in the ventral spiral depression. Its total intercingular displacement is 0.64 of the total length of the body.

The nucleus is ellipsoidal and located slightly above the center of the body. Chromatin threads could not be detected in its contents. Its major and minor axes are 0.69 and 0.36 transdiameter in length respectively.

A long sacklike pusule opens distally into each flagellar pore. The cytoplasm is finely granular. There are a few blue-green refractive spherical oil drops scattered through it, and a large food mass in the center. There were no striations or other markings on the surface. The color of the organism is oil yellow shading to yellow ochre at the apices, with pearl grey massed in the center. A thin-walled, symmetrically elliptical, hyaline cyst enclosed the organism. This was surrounded by a second cyst, slightly larger than the inner one, of the same general appearance and structure. There were no chromatophores and nutrition is evidently holozoic.

Dimensions.—Length, 65μ; transdiameter, 27μ; axes of nucleus, 23μ and 12μ; axes of outer cyst, 80μ and 57μ; of inner, 70μ and 45μ.

Occurrence.—A single individual was taken July 24, 1917, with a No. 25 net, in a haul 2.75 miles off La Jolla, California, from 80 meters to the surface in a surface temperature of 21°9 C.

Activities.—These were limited to rotation within the cyst.

Comparisons.—This species is a member of the *C. distortum* group and is next to *C. distortum* (fig. HH, 9) in the degree of ventral excavation and torsion of the body. It has, however, more of the usual *Cochlodinium* proportions. The asymmetry of the antapex allies it with the *C. helix* (fig. HH, 8).

## **Cochlodinium cereum** sp. nov.

Text figure GG, 5

Diagnosis.—A medium sized species with elongated, ellipsoidal body, its length 2 transdiameters; girdle a descending left spiral of 1.7 turns, displaced 0.94 transdiameter; sulcus with apical and antapical loops and a torsion of one turn; color, yellow. Length, 76μ. Pacific off La Jolla, California, July.

Description.—The body is ellipsoidal, quite elongated, rounded anteriorly, truncate posteriorly, its length 2 transdiameters at the widest part at the middle. The left side is more constricted by the furrows than the right. The epicone exceeds the hypocone in size, its length being greater by about 0.1 of its own length. The epicone is elongate hemispherical, with a length from the proximal and distal ends of the girdle of 0.27 and 0.76 respectively of the total length of the body. The hypocone is less regular in outline than the epicone with a truncate antapex slightly notched by the distal end of the sulcus.

The girdle is a descending left spiral of 1.7 turns and a displacement of 0.94 transdiameter. The proximal transdiameter of its course is nearly transverse, changing to a posterior direction with an angle of 20° to 35° from the transverse plane, flattening again somewhat distally. The furrow has a width of about 0.07 transdiameter and is deeply impressed with smooth borders.

The sulcus invades the epicone in a short loop which fades out below the right side of the apex. It turns posteriorly in a descending left spiral which makes one complete turn about the body, terminating at the right side of the apex with a broad, shallow notch at the postmargin. About 0.4 turn of its course takes place posterior to its distal junction with the girdle. The furrow is shallow, but constricts the body rather deeply in the intercingular area. Its width is about 0.5 that of the girdle, widening at the posterior junction to a slightly greater width than that of the girdle, with a still greater deflection of its sides near the antapex. The anterior flagellar pore is found at the anterior junction of the girdle and sulcus.

The nucleus is a rather small, ellipsoidal body, located posterior to the midplane, near the dorsal side of the body. Its major and minor axes are about 0.52 and 0.36 transdiameter respectively.

The cytoplasm is clear and finely granular and almost entirely free from spherules, vacuoles, and food bodies. The color of the organism is yellow diffused through the cytoplasm. One individual was enclosed in a spheroidal cyst with clear hyaline walls, very much larger than the body.

Dimensions.—Length, 76$\mu$; transdiameter, 38$\mu$; axes of nucleus, 20$\mu$ and 14$\mu$; diameter of cyst, 108$\mu$.

Occurrence.—This was observed July 9, 1904, in a haul made with a No. 12 net, 7 miles off San Diego, California, from 185 meters to the surface.

Comparisons.—This species belongs in the *C. strangulatum* group of the subgenus *Cochlodinium*. It is close to *C. citron* sp. nov. (fig. HH, 12) and has less torsion, lacks radial rhabdosomes, and has a smaller apical region. It lies in the line of differentiation leading to the subgenus *Polydinium*, with 3 to 4 turns of the girdle.

## **Cochlodinium citron** sp. nov.

Plate 7, figure 79; text figure HH, 12

Diagnosis.—A small species with elongated subellipsoidal body, its length 1.71 transdiameters; girdle a descending left spiral of 2.1 turns, displaced 0.88 transdiameter, sulcus without apical loop, torsion of 1.1 turns; color, amber yellow. Length, 48$\mu$. Pacific off La Jolla, California, July, August.

Description.—The body is subellipsoidal, tending towards obovoidal, with broad apices, slightly truncate posteriorly, nearly circular in cross-section, its length 1.71 transdiameters at the widest part at the level of the proximal end of the girdle. The epicone exceeds the hypocone in size. It is elongate hemispherical in shape with symmetrically rounded apex, and a length at the proximal and distal ends of the girdle of 0.35 and 0.85 respectively of the total length of

the body. Posterior to the anterior flagellar pore it diminishes rapidly to a narrow band about 0.2 transdiameter in width, which makes one turn around the body, diminishing distally to a slender point. The anterior portion of the hypocone forms a band somewhat wider than the corresponding part of the epicone, and makes one complete turn above the distal junction of the girdle and sulcus. Posteriorly it is broad and rounded and notched at the left side of the antapex by the distal end of the sulcus.

The girdle is a descending left spiral with a distance from the apex at its proximal and distal ends of 0.35 and 0.85 respectively of the total length of the body. It makes 2.1 turns around the body and is displaced about 0.88 transdiameter. The furrow has a width of about 0.08 transdiameter, narrower distally, and is deeply impressed, undercutting its anterior border and curving gradually out to the posterior one. The sulcus scarcely extends anterior to its proximal junction with the girdle, but continues posteriorly in a descending left spiral of slightly more than one turn and terminates in a notch at the left side of the antapex. It forms a shallow trough with smooth sides, and the width is less than half that of the girdle. The anterior and posterior pores open at the anterior and posterior junctions of the girdle and sulcus respectively.

The nucleus is a spheroidal body filled with moniliform chromatin strands and located in the anterior part of the body, dorsad to the anterior pore. Its axis is 0.53 transdiameter in length.

Small club-shaped pusules open into each flagellar pore. In one specimen examined the posterior pusule was seen filling up with a sudden inrush from the outside surrounding medium.

The cytoplasm is finely granular. In the peripheral zone are numerous, light oriental green rodlets placed perpendicularly to the surface (fig. HH, 12). These are about 7μ in length and arranged quite close together. Inside this zone and longitudinally arranged are about six long slender curved rhabdosomes which persisted when cytolysis had caused the dissolution of the body. Outside of these two regions and in the periphery are numerous blue-green rodlets with larger patches of the same color, quite closely scattered through the peripheral plasm.

The color is an amber yellow shading down to an orange tint at the antapex. A few large patches of yellow color are found near the apex and equatorial region.

Dimensions.—Length, 35–49μ; transdiameter, 25–32μ; axis of nucleus, 13–15μ.

Occurrence.—This was one of the species most frequently taken, occurring in most of the hauls made between July 12 and August 21, 1917, from distances 11, 6, and 4 miles off La Jolla, California, in hauls from 80 meters to the surface and was also found in the surface hauls taken at the end of the pier at the Biological Station. The forms figured came from the hauls made at the last named point.

Comparisons.—This species belongs to the *C. citron* group of the subgenus *Cochlodinium*, characterized by two complete turns of the girdle. It stands closest to *C. clarissimum* (fig. GG, 2), without, however, having the apical loop of the sulcus and the superficial vacuolate zone of the latter species. In its peripheral zone of radial rodlets it recalls the condition in many of the species of *Gyrodinium*.

### **Cochlodinium clarissimum** sp. nov.

Plate 5, figure 60; text figure GG, 2

Diagnosis.—A medium sized species with rotund ellipsoidal body, its length 1.51 transdiameters; girdle a descending left spiral of 2 turns, displaced 0.76 transdiameter; sulcus with apical loop and torsion of 2 turns; color, pale glaucous green. Length, 59μ. Pacific off La Jolla, California, July.

Description.—The body is rotund ellipsoidal with broad, rounded apices, nearly circular in cross-section, its length 1.51 transdiameters at the widest part at the middle. The epicone exceeds the hypocone in size, its length being greater by 0.13 of its own length. It is subhemispherical in shape with broad apex. It has a length from the proximal and distal ends of the girdle of 0.27 and 0.77 respectively of the total length of the body, the distal portion consisting of a narrow band making one complete turn around the body. The hypocone is slightly broader than the epicone, somewhat asymmetrical with broad antapex scarcely notched by the distal end of the sulcus.

The proximal and distal ends of the girdle lie at a distance from the apex of 0.27 and 0.77 respectively of the total length of the body, having a displacement of 0.76 transdiameter. It sweeps around the body in a descending left spiral course of two complete turns. The furrow has a width of about 0.08 transdiameter, and is rather deeply impressed, the excavation undercutting the anterior border and curving gradually out to the posterior one. The anterior flagellar pore opens at the anterior border of the junction of girdle and sulcus, the posterior pore at the posterior border of the distal junction, on the same surface of the body.

The sulcus makes one complete turn above the anterior flagellar pore, passing around the apex and terminating just below it on the ventral surface near the right side. Below the pore it passes directly backward a short distance before turning to the left and continues its course as a descending spiral, making a complete turn before meeting the girdle, beyond which it descends directly to the antapex. It thus makes two complete turns about the body. It forms a narrow trough throughout its course anterior to the posterior flagellar pore, posterior to which it widens to 3.5 times its own width and at the antapex makes a wider flare. The borders are smooth and rounded.

The nucleus is subspheroidal in shape and located in the left side of the equatorial region. Its axis is 0.5 transdiameter in length. Moniliform chromatin strands follow its longitudinal axis in curving lines.

Small club-shaped pusules open into the anterior and posterior flagellar pores. The cytoplasm is clear and finely granular. Beneath the peripheral layer is a zone of vacuolate structure. The vacuoles appear rounded in optical section (fig. GG, 2) and in surface view (pl. 5, fig. 60) as irregularly shaped vacuoles closely pressed together over the entire surface. These seemed to be filled with a pale rhodonite, pink-colored fluid, the intervening spaces being greenish. Outside of this zone is a distinct periplast, appearing as a double-contoured wall. In the central part of the body is a large ellipsoidal, greyish food mass and scattered through the cytoplasm a few small oil globules. The color of the protoplasm is a pale glaucous green distributed throughout. A thin-walled, hyaline cyst enclosed the individual figured.

Dimensions.—Length, 70–74$\mu$; transdiameter, 45–50$\mu$; transdiameter of nucleus, 16–18$\mu$.

Occurrence.—Two individuals were taken on July 5, 1917, with a No. 12 silk net, in a haul 6 miles off La Jolla, California, from 80 meters to the surface and in a surface temperature of 21.4 C. Several individuals were taken the following week from approximately the same place and under the same conditions. It was met again July 11 in a haul 4 miles off La Jolla with a No. 25 silk net from 80 meters to the surface.

Comparisons.—*Cochlodinium clarissimum* belongs to the *citron* group of the subgenus *Cochlodinium*, and like *C. citron* (fig. HH, 12) and *C. faurei* (fig. GG, 4) its girdle forms two complete turns around the body. The apical loop is not found so fully developed elsewhere in this genus and resembles that structure as developed in *Pouchetia*, as, for example, in *P. subnigra*.

It is also peculiar in the genus *Cochlodinium* in the degree of its ectoplasmic differentiation. This differs from the peripheral organization of the cytoplasm in *Gymnodinium,* as developed in *G. dogieli* (fig. AA, 8), in which the vacuolate layer is superficial, with the convexities of the individual alveoli roughening the surface of the body. In *Cochlodinium clarissimum* the alveoli are more deeply imbedded, the pellicle presenting a smooth surface.

### **Cochlodinium conspiratum** sp. nov.

Plate 3, figure 29; text figure GG, 10

DIAGNOSIS.—Small species, body broadly ellipsoidal to obovate, flattened and incised on the left, arched on the right; length 1.2 transdiameters; girdle a descending left spiral of 1.8 turns, displaced 0.7 transdiameter; sulcus with apical and antapical loops and torsion of 0.8 turn; plasma chalcedony yellow. Length, 39$\mu$. Pacific off La Jolla, California, July.

DESCRIPTION.—The body is rotund, subellipsoidal to obovate, widest anteriorly, with its length exceeding its transdiameter by only 0.2. Left face flattened, deeply incised at three points by girdle and sulcus, right side more rotund. The epicone exceeds the hypocone in length by 0.2 total length. The epicone is broadly rounded at the apex as a somewhat flattened hemisphere. It has a length at the proximal and distal ends of the girdle of 0.25 and 0.88 respectively of the total length of the body. The hypocone is somewhat narrower than the epicone with a broad, almost flattened but much contracted antapex. Its length at the proximal and distal ends of the girdle is 0.75 and 0.12 respectively of the total length of the body.

The girdle forms a descending left spiral of 1.8 turns. It joins the sulcus anteriorly 0.25 of the total length of the body from the apex. Its first 0.75 turn is almost horizontal or somewhat deflected anteriorly. It then turns abruptly posteriorly 45° from the horizontal for 0.5 turn, then flattens again almost to the horizontal for the last 0.6 turn around the body to meet the sulcus distally at the right of the antapex. Except in the middle part of its course on the right dorsal side, it lies in a narrow, deep depression or trough with rounded borders. The width of the furrow is 0.07 transdiameter. The anterior flagellar pore is located at the anterior junction and the posterior flagellum slightly below the distal junction, on opposite faces of the body. The transverse flagellum traverses only one turn of the girdle and the posterior flagellum is 0.75 of the length of the body in length.

The sulcus invades the epicone in a curving line to the left of the apex. Below the anterior pore it takes a descending left spiral course of one complete turn, ending near the antapex. After joining the girdle near the antapex its antapical loop makes 0.25 of a turn around the antapex in a *horizontal* plane.

The nucleus is broadly ellipsoidal and is located in the posterior half of the body. Its major and minor axes are 0.5 and 0.4 transdiameter in length respectively. Coarsely beaded chromatin threads, eight across one face, traverse its shorter axis.

A small, sacklike pusule opens anteriorly into the anterior flagellar pore. The cytoplasm is very clear and transparent, though filled with numerous inclusions. Six large, subspherical food masses filled the center of the body. These varied in color from blue to grey green. Mingled with these were a few minute oil droplets and refractive granules. The color is a pale chalcedony yellow with a tinge of yellow ochre near the girdle. The proximal border of the girdle was marked by a bright yellow-green line from which the color diffused into the adjacent cytoplasm.

Dimensions.—Length, 39$\mu$; transdiameter, 31$\mu$; axes of nucleus, 15$\mu$ and 12$\mu$.

Occurrence.—This was taken July 26, 1917, with a No. 25 silk net, 2.5 miles off La Jolla, California, in a haul from 80 meters to the surface, in a surface temperature of 21°6 C.

Comparisons.—This species lies midway between *C. vinctum* (fig. HH, 3) and *C. geminatum* (fig. HH, 1) in the degree of asymmetry and flattening. It has more torsion than *C. vinctum* by nearly 0.5 turn, is only half the size and has a horizontal extension of a longitudinal antapical loop of the sulcus. It is also smaller than *C. geminatum*, lacks its distinct ochraceous chromatophores, and has somewhat more torsion of the sulcus.

This species belongs to the *C. strangulatum* group of the subgenus *Cochlodinium*, resembling other members of that group in the amount of torsion of the body, as indicated by the number of turns of the girdle, but differing from them in the type of spiral formed by the girdle. About 0.5 of the entire length of the girdle encircles the anterior end, giving to the epicone a relatively small proportion of the anterior surface of the body.

## **Cochlodinium constrictum** (Schütt) Lemm.

Text figure GG, 13

*Gymnodinium constrictum* Schütt (1895), pl. 26, fig. $93_1$.
*Cochlodinium constrictum,* Lemmermann (1899), p. 360.

Diagnosis.—A medium sized species with irregularly biconical body, its length 1.38 transdiameters; girdle salient, a descending left spiral of about 0.18 turns, displaced about 0.76 transdiameter; sulcus extending from apex to antapex, with torsion of about 1 turn; color, rose pink. Length, 90$\mu$. Atlantic (?) or Bay of Naples.

Description.—This description of this species is based on a single figure of Schütt (1895, pl. 26, fig. $93_1$), the data of which are inadequate on some points, such as the anterior termination of the sulcus and girdle and the distal end of the girdle. From a comparison of his figure and other species of *Cochlodinium* one may approximately locate the position of the points mentioned. This has been done in the following description.

The body is roughly biconical with rounded apices, salient girdle and constricted sulcus, length 1.38 transdiameters at the widest part, which is submedian. The hypocone exceeds the epicone in size. The epicone has a length probably of about 0.17 above the proximal border of the girdle and from its distal extremity of about 0.7 of the total length of the body. Its sides are unequally rounded with a depression on the dorsal face, which may be the anterior end of the sulcus on the ventral side, incorrectly drawn as on the dorsal surface. The apex is broadly rounded and blunt. The hypocone diminishes to about half its width a short distance below the girdle, beyond which it is rounded with a broad, blunt antapex.

The junction of the girdle and sulcus occurs a short distance below the apex. It follows a descending left spiral course around the body and meets the distal end of the sulcus about 0.3 of the total length of the body from the antapex. The girdle occupies a high, ridgelike portion of the body, from which the surface slopes away on either side. The girdle itself is apparently shallow with smooth borders.

The sulcus occupies the trough between the two high ridges formed by the spiral course of the girdle. It follows a descending spiral course which makes about one turn of the body. The last part of its course is longitudinally directed, terminating at the antapex. The flagellar pores are not figured.

The nucleus is spheroidal and is posterocentrally located. Its axis is about 0.3 transdiameter in length.

The cytoplasm is apparently granular with a few small spherules anterior to the nucleus and is diffusely colored rose pink.

Dimensions.—Length, 90μ; transdiameter, 65μ; diameter of nucleus, 21μ.

Occurrence.—Figured by Schütt (1895) from the material of the Plankton Expedition, presumably from the Bay of Naples or the Atlantic.

Comparisons.—*C. constrictum* is one of the few red or rose colored species of the genus, sharing this feature with *C. archimedes* (Pouchet) Lemm., *C. rosaceum* sp. nov., and *C. radiatum*. It is unlike any other species in the salient ridge in which the girdle lies, this usually being a region of constriction.

## **Cochlodinium convolutum** sp. nov.

Plate 10, figure 115; text figure HH, 5

Diagnosis.—A rather small species with subovoidal body, contracted anteriorly, its length 1.44 transdiameters; girdle a descending left spiral of 1.6 turns, displaced 0.82 transdiameter; sulcus with apical and antapical loops and torsion of 0.8 turn; color, green. Length, 49μ. Pacific off La Jolla, California, July, August.

Description.—The body is subovoidal with broad apices, widest posteriorly, nearly circular in cross-section, its length 1.44 transdiameters at the widest part. The anterior end is rounded, the posterior end deeply excavated by the sulcal notch. The epicone is exceeded in size by the hypocone, its length being greater but its transdiameter less. It is convex-conical with a slight concavity on the dextrodorsal side in the region of the anterior junction of the sulcus and girdle. It has a length from the proximal and distal ends of the girdle of 0.27 and 0.81 respectively of the total length of the body. Its posterior portion is a slender pointed band which makes about 0.6 turn around the body. The hypocone is less symmetrical than the epicone, its ventral face abutting on the girdle and sulcus, usually drawn out in a baglike extension which is separated posteriorly from the dorsal surface by the sulcal notch.

The girdle is a descending left spiral of 1.6 turns and a displacement of 0.82 transdiameter, its proximal and distal ends having a distance from the apex of 0.27 and 0.81 respectively of the total length of the body. The first 0.6 transdiameter of its course is nearly transverse, turning posteriorly with an angle of about 30° with the transverse plane on the sinistrodorsal surface, flattening to a nearly transverse plane in the dextrodorsal surface and again turning posteriorly in the last part of its course on the ventral face. The furrow has a width of about 0.05 transdiameter and is usually deeply impressed with rounded, overhanging borders.

The sulcus invades the epicone in a short wide loop which terminates below the apex on the right side, or it may partly encircle the apex. Beyond the anterior flagellar pore it turns to the left in a descending spiral course with a torsion of 0.8 turn. The furrow is narrow, less than half the width of the girdle, widening slightly posteriorly where it deeply notches the antapex. The anterior flagellar pore is located at the anterior junction of the girdle and sulcus, the posterior pore slightly beyond the posterior junction.

The nucleus shown in the individual in figure 115, plate 10, has the elongated, curved form of the predivision stage. It fills nearly the entire dorsoventral part of the body with a length of about 0.7 of the total length of the body. Other individuals possessed ellipsoidal nuclei with major and minor axes of about 0.6 and 0.5 transdiameter respectively.

Long club-shaped pusules open into either or both flagellar pores or they may be connected at their extremities, forming a complete channel between the two openings. The cytoplasm is clear and transparent and usually contains numerous blue-green spherules in the peripheral zone. Food bodies, grey, yellow or yellow green in color are generally present in the cytoplasm, indicating a holozoic type of nutrition. The general color is grey or greenish with a tinge of yellow ochre near the apices. A thin hyaline cyst often encloses the organism.

Dimensions.—Length, 49–72$\mu$; transdiameter, 34–40$\mu$; axes of nucleus, 16$\mu$ and 13$\mu$; length of cyst, 88$\mu$.

Occurrence.—This was first observed in a surface haul made near the Biological Station at La Jolla, California, July 27, 1914. It was again taken in 1917, in hauls made July 20 and 23, 6 miles off La Jolla, from 80 meters to the surface and in surface temperatures of 21° and 20.7 C respectively, and on August 6, 4 miles offshore, from 60 meters to the surface and a surface temperature of 21.°1 C.

Comparisons.—This species exhibits the same mobility of its posteroventral surface as is found in *C. cavatum* (fig. T, 1), and in *Pouchetia,* as in *P. maculata* (fig. T, 2), forming part of an orthogenetic line of evolution culminating in *Proterythropsis crassicaudata* (fig. T, 3) and in *Erythropsis* (fig. T, 4), where this region is prolonged into a well developed prod, or tentacle. It belongs in the subgenus *Glyphodinium*, near *C. schuetti* nom. sp. nov. (fig. HH, 2) and *C. helix* (Pouchet) Lemm. (fig. HH, 8), differing from both in its greater development of the apical loop of the sulcus and more deeply notched antapex.

## **Cochlodinium distortum** sp. nov.

Plate 7, figure 78; text figure HH, 9

Diagnosis.—Very large species, with labile body deeply concave ventrally, with subequal anterior, median and posterior lobes, apices broadly rounded; girdle a descending left spiral of nearly 1.5 turns, displaced at least 0.42 total length of body; sulcus with about 0.5 turn (morphological); nucleus anterior; surface striae beaded with orange. Length, 155$\mu$. Pacific off La Jolla, California, July.

Description.—The body is profoundly distorted by constrictions which mark off three subequal anterior, median, and posterior lobes and by a deep ventral concavity and dorsal arching of the median lobe, so that the body has the form of a three-lobed kidney. The three lobes are about equal in volume and in diameter, except that the median lobe is somewhat narrower and longer than the others and deficient ventrally; the posterior lobe is perhaps a trifle the largest. The body is also twisted in the direction of the usual torsion of the sulcus, thus adding to the difficulty of interpretation. Its length is 2.25 transdiameters measured across the terminal lobes which are equal in this dimension.

The epicone exceeds the hypocone by 0.08 total length and contains parts of all three lobes. Its length at the proximal and distal ends of the girdle is 0.33 and 0.75 respectively of the total length of the body. The apex is hemispherical. The hypocone has a length of 0.67 and 0.25 total length respectively at the two ends of the girdle and a subhemispherical antapex, somewhat deflected ventrally and slightly flattened on the ventral face posteriorly. The deep concavity affects the intercingular region of these two segments of the body.

The girdle pursues a somewhat erratic course owing to the concavity and torsion of the body. It forms a descending left spiral with a total displacement of 0.45 total length. From its junction with the anterior end of the sulcus it makes 0.5 turn in the horizontal plane, turns posteriorly at the right face along the arched dorsal side of the middle lobe, and upon its contact with the posterior lobe turns again to an almost horizontal, somewhat sinuous course for the last 0.75 turn. Its total course is thus about 1.5 turns. The amount of the torsion and resulting overlap may be greater than this, as is indicated by the course of the surface striae, but its determination is obscured by the ventral concavity. The furrow is 0.06 transdiameter in width, and is not deeply impressed.

The sulcus does not extend anteriorly above the junction with the girdle and is hidden posteriorly in the concavity. It makes about 0.5 turn of a descending left spiral, continues posteriorly below its junction with the distal end of the girdle about half way to the antapex. Its total length in the anterior-posterior direction is 0.56 total length or more, of which 0.42 is intercingular. The anterior pore is at the anterior junction and the posterior one about one width of the furrow below the posterior junction.

The nucleus is a homogeneous ellipsoidal body located almost transversely in the extreme anterior end of the body. Its axes are 0.74 and 0.50 transdiameter in length respectively. A small spherical pusule opens by a short canal anteriorly into the anterior flagellar pore, and a smaller one also opens anteriorly, instead of posteriorly as usual, into the posterior pore. There were no chromatophores, food balls, oil globules, or rhabdosomes. The cytoplasm was remarkably clear and free from coarse vacuolation. The surface was striate with fine greenish yellow lines running longitudinally parallel to the morphological axis from apex to antapex. Scattered along their courses at somewhat regular intervals are numerous orange globules of varying size. They are somewhat more crowded near the girdle and the apices of the body.

DIMENSIONS.—Length, 155$\mu$; transdiameter of terminal lobes, 70$\mu$; axes of nucleus, 50$\mu$ and 37$\mu$.

OCCURRENCES.—One individual taken 4 miles off La Jolla, California, on July 27, 1917, in a haul from 80 meters to the surface in a surface temperature of 21°9 C.

ACTIVITIES.—Both flagella were normally active and the animal moved intermittently with a jerking motion. There was no evidence of abnormality in its activities. The body was exceptionally plastic and labile.

COMPARISON.—This is one of the most aberrant types of the genus *Cochlodinium*, not far from *Gyrodinium* in the amount of torsion, and striate, as is often the case in species of that genus. The location and axial position of the nucleus, together with the deep concavity and distortion of the body, suggests the possibility that this was a form in the telophase of binary fission, but no second nucleus was present in the translucent posterior end. The form also suggests mechanical distortion, but there was no change prior to those which lead to cytolysis and there were none of those evidences of mutilation or abnormality which are readily detected. The form is bizarre, but not clearly abnormal, and its activities were of the normal type.

The species also represents the extreme specialization of a line of species in which the sinistroventral region is deeply incised or concaved by the sulcus and the dextrodorsal one more or less arched. This series progressively includes *C. geminatum*, *C. schuetti* (fig. HH, 2), *C. vinctum* (fig. HH, 3), *C. rosaceum* (fig. HH, 4), *C. convolutum* (fig. HH, 5), *C. helix* (fig. HH, 8), and *C. cavatum* (fig. HH, 10), and culminates in *C. distortum* (fig. HH, 9).

### **Cochlodinium elongatum** sp. nov.

Plate 4, figure 45; text figures O; GG, 7

Description.—The body is long cigar-shaped, its length 3.78 transdiameters at the widest part, which is anterior. It was enclosed in a cyst only very slightly wider than itself but with a somewhat greater length. The cytoplasm is granular, clear and dull opaline green in color. A few refractive rodlets were present near one end (anterior) and a single large vacuole near the other.

When this organism was first observed a *Cochlodinium*-like girdle or furrow followed a spiral course around the body from one end to the other (pl. 4, fig. 45), and the nucleus presented the appearance of a late telophase stage of division, with the chromosomes plainly evident. Shortly after it was first seen the furrow became obliterated and the body divided into two portions (fig. O, 2). A second division of both nucleus and cytoplasm took place (fig. O, 3), followed in a short time by a third division which resulted in the production of eight small bodies within the cyst (fig. O, 4). Further development did not take place, though it was still held under observation for a short time when it began to disintegrate.

A single specimen of this peculiar organism was observed in the plankton at La Jolla and one that was not adequate for clearly determining its systematic position and relationships. Its undoubted girdle, dinoflagellate type of nucleus and peculiar type of division place it with the dinoflagellates and is deemed important enough to record its occurrence here, leaving further investigation to determine its status more fully.

A comparison of our figures (fig. O) and those of Chatton (1906) for *Blastodinium pruvoti* (fig. J) shows a striking similarity between the two forms. In *Blastodinium*, however, according to Chatton, the body is spirally encircled not by a furrow or girdle but by a series of fine spines, linearly arranged. This difference would effectively separate the two forms and this separation is further widened by the ensuing development. In *Blastodinium* the body divides into two portions, and these follow individual lines of development, the body increasing to nearly three times its former size (figs. J, 2, 3, 4), the final result being the production of small *Gymnodinium* (fig. J, 5). No evidence has been found of a similar division of the body into macrocyte and microcyte in our form. It seems then that in spite of close resemblances in form and identity in size these two organisms cannot be considered generically related.

Dimensions.—Length, 174μ; transdiameter, 46μ; length of cyst, 195μ.

Occurrence.—This was taken August 10, 1917, in a haul one mile off La Jolla, California, from 50 meters to the surface, and in a surface temperature of 22°5 C.

### **Cochlodinium faurei** sp. nov.

Plate 2, figure 25; text figure GG, 4

Diagnosis.—A medium sized species with rotund, subovoidal to ellipsoidal body, its length 1.36 transdiameters; girdle a descending left spiral of two turns, displaced 0.78 transdiameter; sulcus with apical and antapical loops and

torsion of 1.2 turns; color, greenish grey. Length, 56μ. Pacific off La Jolla, California, July, August.

Description.—The body is of robust habit, subovoidal to ellipsoidal in shape, moderately constricted by the furrows, circular in cross-section, slightly broader anteriorly, its length 1.36 transdiameters at the widest part. The epicone and hypocone are subequal in size. The epicone is rounded anteriorly or may have the appearance of a broad flat cone, with blunt apex. It has a length at the proximal and distal ends of the girdle of 0.18 and 0.83 respectively of the total length of the body. Its distal portion forms a narrow band anteriorly, becoming wider and again contracting to a slender point distally. The anterior portion of the hypocone is wider than the corresponding part of the epicone, with its sides rounded posteriorly and the antapex deeply notched by the distal end of the sulcus.

The proximal and distal ends of the girdle lie at a distance from the apex of about 0.18 and 0.83 respectively of the total length of the body. It forms a descending left spiral of two complete turns, the first and last parts of its course having a nearly transverse direction for about 1 transdiameter, the remainder of its course forming an angle of 25° to 30° with the transverse plane of the body. The furrow varies slightly in width, its average being about 0.04 and 0.06 transdiameter. It is deeply impressed, often constricting the body, with the excavation undercutting both borders, either of which may be smooth or with an irregular wavy outline.

The sulcus extends anteriorly from the anterior flagellar pore to the left side of the apex in a lightly curved line. After passing the proximal end of the girdle it turns towards the left and sweeps around the body in a descending left spiral which makes slightly more than one turn before meeting the distal end of the girdle, beyond which it follows a straight line to the antapex. Its width is less than half that of the girdle except at the region of the anterior pore and the distal end of the girdle. It expands near the posterior end of the body, deeply notching the antapex. The anterior flagellar pore is found at the proximal end of the girdle, the posterior pore just beyond the distal junction of the girdle and sulcus.

The nucleus is spheroidal to ellipsoidal in shape and is located in the posterior part of the body. It is filled with moniliform chromatin strands. Its axes are about 0.46 and 0.4 transdiameters in length respectively.

The cytoplasm is finely granular, but usually very clear and transparent. Small sacklike pusules may be present at either or at both pores. In one individual the posterior pusule was rather short with two subequal diverticula starting from its proximal end. Food bodies are generally present in the cytoplasm, the individual shown in figure 25, plate 2, having one large yellowish mass centroanteriorly, with several green and dark refractive bodies near it. Small blue-green oil droplets were present in the peripheral zone. The general color of the organism is pearl grey and green, a few individuals showing a yellowish green tone. No striae or other markings could be detected on its surface.

Dimensions.—Length, 55–60μ; transdiameter, 35–41μ; axes of nucleus, 19μ and 16μ.

Occurrence.—A single individual was taken July 20, 1917, with a No. 25 net, 6 miles offshore at La Jolla, California, in a haul from 80 meters to the surface and in a surface temperature of 20°5 C. It was also found July 24, 2.75 miles offshore, and August 17, 0.75 miles offshore, in hauls from 80 meters to the surface and surface temperatures of 21°9 C and 22°5 C.

Comparisons.—This species belongs to the subgenus *Cochlodinium*, a group showing considerable symmetry of form, and stands next to *C. clarissimum* (fig. GG, 2) in size and proportion, but the uppermost part of the epicone is much smaller, the apical loop of the sulcus less developed, its peripheral plasma less differentiated, and its color slightly different.

## **Cochlodinium geminatum** (Schütt) Schütt

Text figure HH, 1

*Gymnodinium geminatum* Schütt (1895), p. 165, pl. 23, fig. 75.
*Cochlodinium geminatum,* Schütt (1896), p. 2, fig. 1.
*C. geminatum,* Lemmermann (1899), p. 360.

DIAGNOSIS.—Small species, body subellipsoidal, its length 1.4–1.67 transdiameters; girdle a descending left spiral of 1.5–2 turns, displaced about 0.8 total length; sulcus with 0.5–1 turn; chromatophores vermiculate, ochraceous; cyst pyriform. Length, 47–75$\mu$. Atlantic or Bay of Naples; Pacific off La Jolla, California, July.

DESCRIPTION.—This is based wholly on Schütt's (1895, 1896) figures, as the species did not occur at La Jolla in 1917 and our earlier notes are uncritical on its morphology. Serious difficulties are encountered in attempting to work out the morphological features from these figures because all of them are based on individuals in chain subject to modifications at fission, such as expansion of the conjoined ends, modification in the distinctness of and course of sulcus and girdle, and possible complications of and changes in torsion. Furthermore, there are wide differences between Schütt's three figures in size and proportions. These appear to be due to the rounding-up prior to cytolysis, but the differences in size, such as exist between his figures $75_2$ and $75_3$ ($75\mu$ and $47\mu$), when correlated with marked differences in torsion (about 0.5 and 1 turn of the sulcus) are at least puzzling and raise the question as to the specific identity of the individuals shown in these two figures. The perplexities are increased when in a later paper (1896) Schütt reverses the orientation of the cyst of his earlier paper (pl. 23, fig. $75_2$) and includes in it his figure $75_3$. On the comparison of Schütt's figure $75_2$ with related species the orientation he uses here (1895) appears to be justified, but it hardly seems probable that the chain could turn end for end, as it must do, if his later orientation of the cyst (1896, fig. 1), containing what appears to be the chain of his earlier (1895) figure, is correctly oriented. In short his (1896) orientation of the cyst about the chain in the later figure is irreconcilable with his earlier (1895) figures. A brief attempt to analyze the morphology of this species follows.

The body is subellipsoidal, wider near the middle, sometimes slightly flattened in the sinistral face and bulging on the dextral; length, 1.40–1.67 transdiameters. Epicone and hypocone subequal. Apex asymmetrically subconical (90°), deflected to the right. Antapex also asymmetrically rounded, subconical to flattened; deflected to the right. The girdle is a descending left spiral of about 1.5 turns (Schütt, 1895, pl. 23, fig. $75_2$), or 2 turns (fig. $75_3$). Its anterior end almost reaches the apex, whence it descends in a fairly uniform spiral to within 0.2 of the total length of the antapex, having a total displacement of nearly 0.8 total length. The furrow is wide, 0.12 transdiameter in width, deeply impressed with overhanging lips. The sulcus is not clearly shown, but appears to run from apex to antapex with a torsion of 0.5–1 turn of a descending left spiral. It is about half the width of the furrow and does not constrict the body. There is no apical loop above the anterior junction with the girdle and the extension beyond the posterior junction is short or lacking.

The nucleus is central, spherical, or broadly ellipsoidal, 0.5–0.7 transdiameter in diameter or major axis, and crowded with moniliform chromatin threads of uniform granules. The ochraceous chromatophores lie uniformly distributed and about equidistant in the peripheral plasma. They are vermiculate rodlets about 0.2 transdiameter in length and with a diameter 0.2 their length. They straighten out and round up into spherules as cytolysis approaches. One or more pusules lie near the anterior flagellar pore.

This species is generally seen in chains of two or four individuals within a pyriform translucent gelatinous cyst whose length is about five times that of the body. Schütt figures this with the broader end posterior in his earlier paper (1895) and anterior in the later one (1896). After treatment with safranin the cyst shows granular concentric laminations surrounding a non-laminate axial region containing the chain.

DIMENSIONS.—Length, 47–75$\mu$; transdiameter, 35–45$\mu$; axes of nucleus, 22$\mu$ and 30$\mu$; length of cyst, 185$\mu$; diameter, 108$\mu$.

OCCURRENCE.—Taken on two occasions in the plankton off La Jolla, California, in 1906, once on July 3, 2.75 miles offshore in a haul of a No. 20 net from 185 meters to the surface in a surface temperature of 20°4 C, and again on July 10 in a surface haul of a No. 12 net, 2 miles offshore in a surface temperature of about 20°9 C. In both instances chains of four individuals were found. On July 10 the species was fairly abundant.

Schütt (1895) figures it presumably from the Bay of Naples or from the collections of the Plankton Expedition in the Atlantic. It has not been reported elsewhere.

ACTIVITIES.—The individuals, both free and in chain, round up and cytolize quickly. Individuals in chain frequently separate when stimulated by the illumination of the microscope. When this occurs in a cyst the remnants will fuse into a single sphere. As cytolysis approaches the surface is wrinkled locally by waves of contraction producing pseudopodia-like elevations. The pellicle becomes detached locally after these contractions, a clear fluid oozes out at the flagellar pores, along the furrows and elsewhere, and when the pellicle about the now spheroidal mass ruptures the cytoplasm flows out and is speedily dissolved.

COMPARISONS.—Too little is critically known of this species for comparisons. It is not far from *C. conspiratum* (fig. GG, 10) on the one hand and *C. catenatum* (fig. GG, 14) on the other. The latter tends to form chains, but is smaller, appears to have less torsion, 0.5 turn only, and less intercingular displacement, 0.6 instead of 0.8 total length, and to be nearly colorless instead of having ochraceous chromatophores. *C. geminatum* is more elongated and less incised than *C. conspiratum* and has chromatophores, which the latter lacks. Note should be made of the fact that the more elongate individuals with two turns of the girdle which Schütt (1895, pl. 23, fig. $75_3$) figures are very close to *C. archimedes* (Pouchet) Lemm. (fig. HH, 17) in size, proportions, and torsion, and should be classed with it were it not for the implication which Schütt's (1896) later figure raises, that it is a phase of the chain of his other figure (fig. $75_2$) in which prior to fission the torsion has increased 0.5 turn and the girdle and sulcus have elongated considerably. It is the least distorted member of the *C. distortum* group of the subgenus *Glyphodinium* and might equally well be placed in the *C. citron* group of the subgenus *Cochlodinium*.

SYNONYMY.—This species was figured by Schütt (1895) as *Gymnodinium geminatum,* but noted later by him (1896) as a *Cochlodinium*.

### **Cochlodinium helix** (Pouchet) Lemm.

Plate 9, figure 92; text figure HH, 8

*Gymnodinium helix* Pouchet (1887), pp. 94–96, fig. 1.
*G. helix,* Schütt (1895), pp. 59, 71, pl. 24, figs. $77_{1-5}$ (fig. $77_6$ is *Cochlodinium schuetti* nom. sp. nov.).
*Cochlodinium helix,* Lemmermann (1899), p. 360.
*Gymnodinium helix,* Entz, Jr. (1907), p. 11; (1909), p. 246.
*Cochlodinium helix,* Paulsen (1908), p. 103, fig. 143.
*C. helix,* Lebour (1917*b*), p. 103.

Diagnosis.—A small species with subovoidal asymmetrical body, its length 1.42 transdiameters; girdle a descending left spiral of 1.5 turns, displaced 0.65 transdiameter; sulcus with apical and antapical loops and a torsion 0.8 turn; color, dull yellow green. Length, 54μ. Atlantic off Concarneau, France; Plymouth Sound, England, August; Pacific off La Jolla, California, July, August.

Description.—The body is irregularly subovoidal, broad and asymmetrical posteriorly, nearly circular in cross-section, its length 1.42 transdiameters at the widest part in the lower hypocone. The anterior end is tapering, the posterior broad, the posteroventral face drawn out into a flaplike extension on its morphological right side, giving to the body a sinistroventral excavation, with the dorsal side strongly convex. The epicone and hypocone are subequal in size. The epicone is convex-conical, about 45° anteriorly, with blunt apex. It has a length from the proximal and distal ends of the girdle of about 0.21 and 0.84 respectively of the total length of the body. The hypocone is broader than the epicone, less symmetrical, the dextroventral face drawn out into an outstanding flap or lobe, still further marked off posteriorly by the deep sulcal notch.

The girdle is a descending left spiral of 1.5 turns, displaced about 0.65 transdiameter. The anterior part of its course is nearly transverse, turning posteriorly on the left side at an angle which flattens to a nearly transverse plane at the dorsal margin, crossing the right transversely and turning posteriorly around the outstanding flap which is composed of portions of both epicone and hypocone. The furrow has a width of less than 0.05 transdiameter and is lightly impressed with rounded borders.

The sulcus invades the epicone in a short loop which may partly encircle the apex or may terminate below the right side. It passes posteriorly in a left spiral direction, its torsion about 0.8 turns. It deeply constricts the body in the intercingular area, lying at the base on the left side of the outstanding flaplike portion of the body. It meets the distal end of the girdle at the posterior point of emergence of the flap from the main body. The furrow is somewhat narrower than the girdle. The anterior and posterior flagellar pores are found at the anterior and posterior junctions of the girdle and sulcus respectively.

The nucleus is spherical to ellipsoidal in outline and is located in the posterior portion of the body. It is filled with fine, moniliform chromatin strands. Its axis is about 0.4 transdiameter in length.

The long, sacklike pusules opening into each flagellar pore are connected at their extremities, forming a tubular canal between the two openings. The cytoplasm is finely granular. The centroanterior portion of the body was occupied by a pale dull yellow green food mass. Blue-green spherules are usually abundant in the peripheral zone. The general color of the organism is dull yellow green with a tinge of orange in the posterior part. A thin-walled, hyaline, nearly circular cyst enclosed the organism.

DIMENSIONS.—Length, 45–54$\mu$; transdiameter, 31–35$\mu$; axes of nucleus, 15–20$\mu$ and 12$\mu$; diameters of cyst, 50$\mu$ and 53$\mu$.

OCCURRENCE.—Two individuals were taken July 27, 1917, 4 miles off La Jolla, California, in a haul from 80 meters to the surface and in a surface temperature of 21°9 C. It was also present August 15 in a haul 0.75 mile offshore, from 70 meters to the surface.

It was described by Pouchet (1887) from the Atlantic off Concarneau, France, where it was abundant from April 29 to May 3. It has also been recorded from Plymouth Sound, England, by Lebour (1917*b*) in August.

SYNONYMY.—Figured by Pouchet (1887) as *Gymnodinium helix,* the name was changed by Lemmermann (1899) to *Cochlodinium helix.* Schütt (1895) figures under the *Gymnodinium helix* Pouchet two distinct forms. His figures $77_{1\text{-}5}$, plate 24, agree in all essential details with Pouchet's species. His figure $77_6$, however, is distinct in shape, torsion, and formation of the posterior end of the body. Both of these forms we have found in our material at La Jolla, and have no difficulty in separating them. His figure $77_6$ we therefore reject from *Cochlodinium helix* and place it in our new species, *C. schuetti.*

COMPARISONS.—This species, like *C. cavatum* sp. nov. (fig. HH, 10), shows the greatest extent to which the mobility of the posteroventral portion of the body is developed in this genus. It probably lies in the direct line of evolution which has produced *Proterythropsis,* and *Erythropsis* (fig. T) with this region of the body still further differentiated in the tentacular recess and the tentacle or prod. It belongs between *C. convolutum* (fig. HH, 5) and *C. cavatum* (fig. HH, 10), as shown by the degree of asymmetry of the body.

## **Cochlodinium lebourae** sp. nov.

Plate 2, figure 23; text figure HH, 7

DIAGNOSIS.—A small species with ellipsoidal body, its length 1.66 transdiameters; girdle a descending left spiral of 1.7 turns, displaced 0.83 transdiameters; sulcus with apical and antapical loops, and torsion of 1.5 turns; color, pale lumiere green. Length, 50$\mu$. Pacific off La Jolla, California, July.

DESCRIPTION.—The body is elongate, subellipsoidal, contracted posteriorly, somewhat constricted by the girdle, nearly circular in cross-section, its length 1.66 transdiameters at the widest part below the middle. Both apices are broad, the anterior rounded, the posterior notched by the sulcus. The epicone is considerably larger than the hypocone, its length being greater by 0.23 of itself. It is elongate hemispherical in shape with a length from the proximal and distal ends of the girdle of 0.3 and 0.84 respectively of the total length of the body. Its posterior portion consists of a narrow band tapering to a slender point distally. The hypocone is more irregular in shape and consists of a wide band which makes slightly more than one turn around the body and a rounded distal portion which is broadly excavated on the ventral surface by the distal end of the sulcus. The most posterior segment of the hypocone is only 0.6 of the width of the one above it.

The girdle is a descending left spiral of 1.7 turns and a displacement of 0.83 transdiameter. The proximal and distal portions of its spiral form angles of about 10° with the transverse plane,

steepening to about 30° in the middle part of its course. The furrow has a width of about 0.05 transdiameter and is deeply impressed with overhanging borders. With the sulcus it constricts the body somewhat, giving to it a lightly lobed outline.

The sulcus invades the epicone in a wide loop which terminates at the right side of the apex. It makes an abrupt turn to the left after passing the anterior flagellar pore, and sweeps around the body spirally with a torsion of 1.5 turns in reaching the antapex. It is narrow anteriorly and in the intercingular area, widening posteriorly to about three times the width of the girdle. Its constriction of the body is somewhat less than that of the girdle. The anterior flagellar pore is found at the anterior junction of the girdle and sulcus, the posterior pore about one transdiameter beyond the distal junction, thus placing it on the same side of the body as the anterior pore.

The nucleus is a subellipsoidal body filled with fine, moniliform chromatin strands following its longer axis. It is located in the posterocentral part of the body, slightly oblique to the transverse plane. Its major and minor axes are about 0.63 and 0.43 transdiameter in length respectively.

The long sacklike pusules opening into the two flagellar pores are connected at their extremities by a slender canal. The cytoplasm is very clear and transparent and contains food bodies and numerous blue-green oil globules in the peripheral zone. The general color of the organism is pale lumiere green. It was enclosed in a thin-walled, slightly distended, hyaline cyst.

Dimensions.—Length, 50μ; transdiameter, 30μ; axes of nucleus, 19μ and 13μ; length of cyst, 58μ.

Occurrence.—A single individual was observed July 20, 1917, taken in a surface haul at the end of the pier at the Biological Station at La Jolla, California.

Comparisons.—This species belongs to the subgenus *Cochlodinium,* and in its type of girdle and torsion is not unlike *C. citron* (fig. HH, 12), but lacks its rhabdosomes and has a more contracted antapex.

Named after Miss Marie Lebour, the investigator of the Gymnodinioidae of British waters.

### **Cochlodinium miniatum** sp. nov.

Plate 10, figure 107; text figure GG, 6

Diagnosis.—A large species with ellipsoidal-fusiform body with minute apical and larger antapical process, its length 2.4 transdiameters: epicone and hypocone subequal; girdle with 1.5 turns, displaced 0.6 total length; sulcus abruptly looped about apex, extending nearly to antapex; nucleus with perinuclear zone; surface of epicone and hypocone unequally striate; pale green yellow blotched with scarlet. Length, 205μ. Pacific off La Jolla, California, July.

Description.—The body is elongated ellipsoidal-fusiform in outline, circular in cross-section, its total length about 2.3 to 2.4 transdiameters (1.7 in contracted forms) at the widest part. Excluding the apical and antapical prolongations, the ellipsoidal midbody has its major axis about twice its minor one and is almost symmetrical, being somewhat more tapering posteriorly and locally modified by the constricting effect of the furrows. The dorsoventral and transdiameters are equal and the epicone and hypocone are nearly so. The steep spiral course of the girdle makes proportional measurements complicated. On its left side its length is 0.5 and on the right 2 transdiameters. The apex is a small conical point about a girdle width in diameter and height, partially encircled by the faintly developed anterior end of the sulcus.

The hypocone on its left side has a length of 1.85 and on its right of 0.45 transdiameters. It is thus a trifle smaller than the epicone.

The girdle is a descending left spiral of 1.5 turns, displaced about 0.6 of the total length of the body. It turns posteriorly at an angle of about 45° with the transverse plane, but the angle gradually becomes less, the latter part of its course having a slope of 30°. The furrow has a width of about 0.06 transdiameter and is deeply impressed with its trough undercutting the anterior border. The anterior end of the sulcus forms an apical loop which passes around the short anterior process at the apex terminating on the right side. It passes posteriorly as a very slender, faintly developed furrow, until it reaches the proximal end of the girdle, where it suddenly expands and for the rest of its course has a width somewhat more than half the width of the girdle, with a deeply impressed furrow, fading out before reaching the antapex. The intercingular portion makes a turn of 0.5 transdiameter. The complete torsion is difficult to estimate, as the anterior loop reverses its usual direction and passes from right to left around the apical process, turning again to the left in the usual direction near the anterior pore region. The posterior portion also swings to the right beyond the posterior pore. The anterior and posterior flagellar pores are located at the anterior and proximal junctions of the girdle and sulcus respectively.

The nucleus is a spheroidal body lying near the center, slightly posterior to the midplane. It is differentiated into two zones, an outer, clear, hyaline perinuclear zone and an inner region filled with coarse moniliform chromatin strands. The outer zone is narrow, about 0.07 of the total transdiameter of the nucleus in width, and is composed of alveoli surrounded by a double-contoured membrane. The axis of the nucleus is about 0.5 transdiameter of the body in length.

The cytoplasm is clear and transparent and pale greenish yellow in color. A number of food vacuoles were present, one of irregular shape and of a pale brown color near the posterior pore close beside the nucleus, and several spherules of varying sizes, bluish or pink in color, scattered through the anterocentral part of the body. Nutrition, as in most if not all of the species of *Cochlodinium*, is holozoic. In the posterior region were two long, slender, blue-green rhabdosomes, about 0.8 transdiameter in length, lying in the plane of the surface with their ends at the antapex.

The surface is finely striate with equidistant, blue-green, broken lines, about 45 on the ventral face of the epicone at the girdle. These are about four times as numerous on the epicone as on the hypocone. Irregular splashes of scarlet pigment are scattered through the peripheral layer in close relation to the striae, but not confined to single lines as in *Gyrodinium corallinum* (pl. 10, fig. 117). These are confined almost exclusively to the epicone in the individual figured.

Dimensions.—Length, 175–205μ; transdiameter, 85μ; axis of nucleus, 45μ.

Occurrence.—Taken on July 9, 1907, in a haul made with a No. 12 net from 120 meters to the surface, 2.5 miles off La Jolla, California, in a surface temperature of about 20° C.

Comparisons.—In its red pigment and type of nuclear structure this species resembles *Gyrodinium corallinum* (pl. 10, fig. 117), *G. virgatum* (pl. 10, fig. 112), and *Gymnodinium rubrum* (pl. 8, fig. 86). With *Cochlodinium strangulatum* (fig. GG, 8) it is the largest species in this genus and next to the largest thus far described in the Gymnodinioidae, *Gymnodinium cucumis* (fig. Y, 16), 210μ in length, alone exceeding it.

It forms the type of a large group of species of the subgenus *Cochlodinium* characterized by a torsion of the body represented by 1.5 turns of the girdle. This amount of torsion places the group near the genus *Gyrodinium,* and in the case of *Cochlodinium minatum* this relationship is still further strengthened by the striate surface, characteristic of many species of *Gyrodinium.*

### **Cochlodinium pellucidum** Lohmann

Text figure GG, 15

*Cochlodinium pellucidum* Lohmann (1908), p. 264, pl. 17, fig. 21.
*C. pellucidum,* Paulsen (1908), pp. 104, 105, fig. 145.
*C. pellucidum,* Ostenfeld (1913), p. 338.
*C. pellucidum,* Lebour (1917*b*), p. 197.

Diagnosis.—A small species with slightly obovoidal body, its length 1.77 transdiameter; girdle a descending left spiral of 1.5 turns, displaced 1.09 transdiameters; sulcus (?); colorless. Length, 39µ. Baltic near Kiel, Germany, June.

Description.—The body is elongate obovoidal with broad apices, widest near the middle, its length 1.77 transdiameters at the widest part. The epicone and hypocone are subequal. In Lohmann's figure the sulcus is omitted entirely, and the girdle drawn as a spiral of 1.5 turns. It is difficult to determine the ends of the girdle, as both the proximal and distal portions of the furrow may be parts of the sulcus. In our description we have taken the length of the girdle as 1.5 turns. This would give to the epicone a length from the proximal and distal ends of the girdle of 0.12 and 0.79 respectively of the total length of the body. The hypocone is slightly narrower than the epicone and is less symmetrical.

The girdle is a descending left spiral of 1.5 turns, its proximal and distal ends distant from the apex about 0.12 and 0.79 respectively of the total length of the body. The furrow is narrow and deeply impressed.

The cytoplasm contains numerous minute spherules scattered through the peripheral zone. In the posterocentral part is a small spheroidal body. Anterior to this is a somewhat irregular ellipsoid, yellow ochre in color, which is probably a food body. In the anterocentral part is another body, dark, slightly smaller than the food mass and ellipsoidal in shape. This is probably the nucleus, though no clue to its identity is given. The organism is colorless.

Dimensions.—Length, 39µ; transdiameter, 22µ.

Occurrence.—Figured by Lohmann (1908) from the Baltic Sea near Kiel, Germany, in June.

Comparisons.—With the sulcus omitted the description of this species is somewhat inadequate. It is, however, tentatively placed in the *C. strangulatum* group of the subgenus *Cochlodinium.*

### **Cochlodinium pirum** (Schütt) Lemm.

Plate 9, figure 101; text figure GG, 3

*Gymnodinium pirum* Schütt (1895), p. 166, pl. 23, fig. $76_{1-4}$.
*Cochlodinium pirum,* Lemmermann (1899), p. 360.
*Gymnodinium pirum,* Entz (1907), p. 11.
*G. dirum,* Entz (1909), p. 246, *lapsus.*

Diagnosis.—Medium sized species; body obovoidal; wider posteriorly; length, 1.6–1.7 transdiameters, girdle a descending left spiral of 1.5 turns, displaced 0.5–0.6 total length; sulcus with torsion of 0.5 turn; surface striate (?); color, yellow ochre. Atlantic; Pacific off La Jolla, California, July.

Description.—The body is ovoidal, somewhat flattened ventrally, widest 0.65 total length from apex. The dorsoventral diameter is 0.84 the transdiameter, which is greatest slightly below the middle. The epicone exceeds the hypocone by 0.15–0.20 total length. Its length at the proximal and distal ends of the girdle is 0.28 and 0.86 total length respectively. It is rotund, subconical (40°), with rounded apex. The hypocone has a length at the proximal and distal ends of the girdle of 0.72 and 0.14 total length respectively. It is wider and fuller than the epicone, flattened hemispherical, and its postmargin is indented by a broad sulcal notch.

The girdle forms a descending left spiral of 1.5 turns. It leaves the anterior junction with the sulcus at 0.28–0.39 total length from the anterior end and is but slightly deflected in the first 0.5 turn, then steepens to 30°–35°, increasing to 45° near the distal end. Its total displacement is 0.50–0.57 of the total length. The furrow is moderately impressed, with distinctly lined edges and slightly overhanging lips. Its width is about 0.1 transdiameter. The sulcus begins near the apex on the epicone, runs thence posteriorly with slight torsion to its anterior junction with the girdle 0.28–0.39 total length from the anterior end, descends with increasing torsion in a steep left spiral of about 0.5 turn to the distal junction 0.14–0.18 total length from the posterior end. In the lower part of the intercingular section it is very close to the girdle. It is a narrow trough about 0.5 width of the furrow and does not lie in a depression of the surface produced by its constriction. Below the posterior junction it flares widely and broadly notches the postmargin. The anterior flagellar pore lies at the anterior junction and the posterior pore some distance below the posterior one. The transverse flagellum runs the whole length of the girdle and the posterior one is less than a transdiameter in length (in the cyst).

In both Schütt's (1895) specimen and our own the nucleus was peculiar in that it was stout reniform in outline with more or less concentric, spiral, moniliform chromatin threads. It lies to the right and near the middle of the body or below it. Its major and minor axes in our specimen were 0.9 and 0.5 transdiameter respectively, in Schütt's specimen (1895), 0.54 and 0.40 respectively. In Schütt's figure (1895) there is a food mass anteriorly and a cluster of twisted rodlets near the apex. The plasma of our specimen was clear, without formed contents of either of these kinds. An anterior sack-shaped pusule opens anteriorly into the pore of the transverse flagellum. No posterior pusule was noted. Schütt (1895) apparently figures both, but does not label them. In the peripheral plasma is a layer of circular ochraceous platelets resembling chromatophores in color. They are uniform in size, regularly distributed and are about 0.5 furrow's width in diameter.

We find no striae on our specimen on close examination. Schütt figures 15 across the ventral face, following the torsion of the body and sparingly beaded. Both Schütt's specimen and our own were enclosed in a large, spheroidal, double-contoured, hyaline cyst, 1.5 length of the body in diameter.

Dimensions.—Length, 60–84$\mu$; transdiameter, 35–50$\mu$; axes of nucleus, 32$\mu$ and 21$\mu$, 27$\mu$ and 20$\mu$. The second figure in each case is of Schütt's specimen.

Activities.—Our specimen was first seen at 4 p.m. in a plankton catch taken at 8 a.m. At 6 p.m. it was still active, circling within the cyst incessantly *without* a single observed rotation, in anticlockwise circles. The transverse flagellum was active during this circling.

Occurrence.—This was first observed July 5, 1917, in a haul 6 miles off La Jolla, California, from 80 meters to the surface and in a surface temperature of 21°9 C. It was also observed in hauls made July 23, 6 miles offshore, from 80 meters to the surface, on July 27, 4 miles offshore, from 80 meters, and on August 20, 0.75 mile offshore in temperatures ranging from 20°8 C to 21°9 C.

COMPARISONS.—This species is a member of the *C. miniatum* group of the subgenus *Cochlodinium*. It is very near *C. convolutum* (fig. HH, 5), but has less torsion, 0.5 instead of 0.6, and less displacement of the girdle, 0.5–0.6 instead of 0.6 total length, and is more ochraceous and less greenish in color. It is larger than *C. schuetti* (fig. HH, 2) and tapers more anteriorly.

## **Cochlodinium pulchellum** Lebour

Plate 7, figure 80; text figures HH, 13, 14, 16

*Cochlodinium pulchellum* Lebour (1917*b*), p. 197, fig. 14.
*C. pulchellum*, Kofoid and Swezy (1917), pp. 90–91, figs. 3, 4.

DIAGNOSIS.—A minute species with body symmetrically fusiform, deeply constricted by girdle and sulcus; its length 2.9 transdiameters; girdle a descending left spiral of 3.2 turns, displaced 0.76 total length; sulcus with torsion of 0.5 turns; color, pale green to glaucous blue. Length, 38$\mu$. Atlantic, Plymouth Sound; Pacific off La Jolla, California, July, August.

DESCRIPTION.—The body is slender, nearly symmetrically fusiform, widest at the middle, very deeply incised and constricted by the girdle and sulcus, its length 2.9 transdiameters at the widest part near the middle. The body tapers a trifle more posteriorly than anteriorly. The epicone exceeds the hypocone in size, its length being greater by 0.1 total length. It has a hemispherical apex slightly deflected to the left, and a length at the proximal and distal ends of the girdle of 0.18 and 0.88 respectively of the total length of the body. The hypocone is about half the width of the epicone anteriorly because the sulcus lies nearer the upper than the lower turn of the girdle and follows its course around the body. Below the distal junction of girdle and sulcus it enlarges into the hemispherical antapex, which has no sulcal notch in the postmargin.

The girdle joins the antapex about 0.18 of the total length of the body from the apex. It sweeps around the body in a descending left spiral of 3.2 turns which steepens from 20° to 30° below the horizontal beyond the first 0.5 turn and joins the sulcus distally about 0.88 of the total length of the body from the apex. Its total intercingular displacement is 0.76 of the total length. It lies in a wide, deep depression with smooth overhanging lips on both sides. The anterior flagellar pore is located at the anterior junction of the girdle and sulcus, the posterior pore slightly beyond the posterior junction.

The sulcus invades the epicone in a short curved loop directed toward the left of the apex. Below the anterior pore it sweeps down in a gradually steepening descending left spiral of 2.5 turns, terminating near the antapex in a small, oblique, antapical loop which makes 0.5 turn beyond the posterior junction with the girdle. It forms a narrow, deep trough with high, rounded sides.

The nucleus is spheroidal and median or somewhat postmedian in position. Its chromatin contents could not be traced. Its diameter is about 0.5 transdiameter in length.

The cytoplasm is coarsely granular and contains from few to numerous, minute oil droplets and sometimes highly refractive greyish bodies. The color ranges from a light pale cendre green to glaucous blue, diffused throughout the cytoplasm. No striations or other surface markings could be detected.

Two individuals were observed within very delicate, transparent cysts slightly larger and conformable to the outline of the body. Both were undergoing binary fission with the nuclei divided in each case.

DIMENSIONS.—Length, 30–40$\mu$; transdiameter, 13–18$\mu$; diameter of nucleus, 7–9$\mu$.

OCCURRENCE.—The first individual of this species was taken July 20, 1917, in a haul made 6 miles off La Jolla, California, from 80 meters to the surface in a surface temperature of 20°5 C. The dividing specimen was taken in a similar haul 4 miles off La Jolla in a surface temperature of 20°8 C. The species was also taken August 3, 6.5 miles off La Jolla in a haul from 80 meters to the surface at 21°2 C and August 13, 0.75 mile offshore in a haul from 83 meters to the surface at about 22°5 C. Miss Lebour (1917*b*) reports a single individual in August, 1915, from the plankton of Plymouth Sound from a water sample taken from a depth of 7 fathoms.

ACTIVITIES.—Encysted forms are incessantly active, rotating within the cyst, both flagella being active.

COMPARISONS.—Miss Lebour describes her specimen as colorless, fusiform in shape, with a girdle of three turns and sulcus making over one turn around the body. She states that its length is 50$\mu$ and that of the cyst 650$\mu$ [*sic*]. These dimensions do not agree with the measurements of her figure which has a length of 60$\mu$ and a width of 21$\mu$, while the length of the cyst is only 85$\mu$. Her figure is evidently reversed, as it shows the organism with a complete reversal of organelles, its girdle and sulcus having a right instead of left descending course (see Kofoid and Swezy, 1917). The sulcus or longitudinal furrow makes 2.5 turns around the body rather than "over one" turn, as she has stated.

This is the smallest species of *Cochlodinium*, although not the shortest, thus lying at the opposite extreme from *C. augustum* (fig. HH, 15), the nearest related species and the only other one in the subgenus *Polydinium*. *C. pulchellum* has 0.5 less turn of the sulcus than *C. augustum* and an oblique instead of a vertical antapical extension of the sulcus beyond the posterior junction with the girdle. Otherwise the principal difference between the two species is in size.

### **Cochlodinium radiatum** sp. nov.

Plate 6, figure 67; text figure GG, 12

DIAGNOSIS.—This is a medium sized species with rotund ellipsoidal body, its length 1.28 transdiameters; girdle a descending left spiral of 2 turns, displaced 0.75 transdiameter; sulcus with torsion of 1 turn; color, glaucous blue splashed with aster purple. Length, 68$\mu$. Pacific off La Jolla, California, July, August.

DESCRIPTION.—The body is of robust habit, rotund ellipsoidal in shape, circular in cross-section, with broad rounded apices, its length 1.28 transdiameters at the widest part at the middle. The epicone exceeds the hypocone in size, its length being greater by 0.3 of its own length. It is subhemispherical in shape, with a length from the proximal and distal ends of the girdle of 0.33 and 0.91 respectively of the total length of the body. The posterior portion is a wide band which diminishes distally to a slender point after making a nearly complete turn about the body. The anterior part of the hypocone is wider than the corresponding part of the epicone, becoming narrower near the posterior pore. It is broadly rounded distally with the

antapex scarcely notched by the distal end of the sulcus. The antapex is somewhat broader and more flattened than the apex.

The girdle has a distance from the apex at its proximal and distal ends of about 0.33 and 0.91 respectively of the total length of the body. It is a descending left spiral of two turns with a displacement of 0.75 transdiameter. The first 1.2 transdiameter of its course is in a nearly transverse plane, turning posteriorly with an angle of 30° to 20° from the transverse plane, the latter 0.5 transdiameter again rising to a nearly transverse direction. It meets the sulcus distally at a distance from the antapex of less than 0.1 of the total length of the body. The furrow varies slightly in the width, being widest in the middle, where its width is about 0.04 transdiameter, and narrower at its proximal and distal ends, and is deeply impressed, undercutting its anterior lip and sloping gradually out to the posterior one. The body is slightly constricted by the furrow on the left side and on the right the borders are slightly elevated above the surrounding surface.

The sulcus begins near the apex as a wide, shallow furrow, which passes posteriorly as a descending left spiral of slightly more than one turn. After passing the anterior pore it contracts to less than half its width above, expanding again after passing the posterior pore into a broad, shallow trough, which fades out at the antapex. The anterior and posterior pores are located at the anterior and posterior junctions of the girdle and sulcus respectively.

The nucleus is elongate ellipsoidal in form, located on the right side of the posterocentral part of the body. It is filled with fine, moniliform chromatin strands. Its major and minor axes are about 0.6 and 0.27 transdiameter in length respectively.

A long, slender pusule connects the anterior and posterior flagellar pores, forming a complete channel between the two openings. The cytoplasm is finely granular and a mixture of pearl grey and light glaucous blue in color. The specimen figured was unusually free from oil droplets. One large food mass, green and yellow ochre in color, was present in the anterior region. There were two groups of long, slender, tapering, greenish, radial rodlets, one of which was in the anterior part near the food mass and the other in the posterior region. Lying in the periphery, and scattered over the entire body, are irregular splashes of pigment, aster purple in color, the larger masses showing a deeper tone than the smaller, lighter ones. A thin hyaline cyst, slightly larger than the body, enclosed one individual.

Dimensions.—Length, 68–78$\mu$; transdiameter, 52–60$\mu$; axes of nucleus, 33–36$\mu$ and 14$\mu$; length of radial rodlets, 12–18$\mu$.

Occurrence.—The specimen figured was taken July 25, 1917, with a No. 25 silk net in a haul 11 miles off La Jolla, California, from 80 meters to the surface and in a surface temperature of 21°2 C. A second individual was taken August 10 with the same apparatus 1 mile off La Jolla in a haul from 50 meters to the surface and in a surface temperature of 21°9 C.

Comparisons.—The most striking feature of this species is its color of irregular, chromatophore-like splotches of aster purple. This is unlike that of any other species of the genus and finds its counterpart in *Gymnodinium violescens* (pl. 6, fig. 69) and *G. lineopunicum* (pl. 6, fig. 65). No observations of the motility of the pigment were made, but it is probable that it possesses that characteristic in common with the pigment of *G. lineopunicum* and *Gyrodinium ochraceum* (pl. 7, fig. 76).

*Cochlodinium radiatum* falls in the *C. citron* group of the subgenus *Cochlodinium*, and lies midway between *C. virescens* (fig. HH, 11) and *C. citron* (fig. HH, 12) in the amount of torsion of the body as shown in the length of the girdle.

## **Cochlodinium rosaceum** sp. nov.

Plate 8, figure 85; text figure HH, 4

DIAGNOSIS.—A medium sized species with ellipsoidal body, its length 1.48 transdiameters; girdle a descending left spiral of 1.5 turns, displaced 0.85 transdiameter; sulcus with torsion of 0.5 turn; color, rose red. Length, 63μ. Pacific off La Jolla, California, July.

DESCRIPTION:—The body is rotund ellipsoidal, with broad apices, nearly circular in cross-section, the dorsal side more convex than the ventral, its length 1.48 transdiameters at the widest part. The epicone exceeds the hypocone in size, its length being greater by 0.26. The epicone is subhemispherical in shape, with a length from the proximal and distal ends of the sulcus of 0.28 and 0.88 respectively of the total length of the body. The hypocone is rounded, with broad, somewhat flattened antapex indented by a wide sulcal notch.

The girdle is a descending left spiral lying at a distance from the apex of 0.28 and 0.88 respectively of the total length of the body. In the first transdiameter of its course it is deflected anteriorly, gradually turning posteriorly at an angle of about 35° with the transverse plane. At its distal end its direction is nearly transverse. The furrow is narrow, varying somewhat in width, its average about 0.04 transdiameter, and is rather shallow, with smooth borders. The sulcus arises near the apex and extends posteriorly in a left, spirally deflected course with a torsion of slightly more than 0.5 turn. The furrow is narrow in width and shallow, but in the intercingular area it lies at the base of a deep constriction of the body, and expands at the antapex in a broad sulcal notch. In figure 85, plate 8, the body is distended by an ingested *Pouchetia,* and the outline is somewhat distorted. Figure HH, 4, gives the appearance of the normal individual. The anterior and posterior flagellar pores open at the anterior and posterior junctions respectively of the girdle and sulcus, lying on opposite faces of the body.

The nucleus is an ellipsoidal body filled with moniliform chromatin strands. It is located in the anterocentral part of the body. Its axes are about 0.5 and 0.3 transdiameter in length respectively.

Small club-shaped pusules are present at either or both pores. The cytoplasm is very clear and transparent, without granulations. Scattered irregularly throughout were salmon-pink globules, evidently containing the same fluid as found in the pusules. The individual shown in figure 85, plate 8, had ingested a *Pouchetia,* probably *rubescens.* This was enclosed in a food vacuole and still preserved part of its girdle, the nucleus and ocellus and its rose coloring. The general color of the organism is very dilute rose red, diffused through the cytoplasm. A few granules of rose red were collected near both apices with larger masses of the same coloring in the central region. A cyst had been recently formed about the body, only slightly larger than itself and closely following its outlines.

DIMENSIONS.—Length, 62–69μ; transdiameter, 43–52μ; axes of nucleus, 20–23μ and 16–18μ.

OCCURRENCE.—Two individuals were taken July 12, 1917, with a No. 25 silk net in a haul made 6 miles off La Jolla, California, from 80 meters to the surface and in a surface temperature of 20°5 C.

COMPARISONS.—*Cochlodinium rosaceum* forms one of a relatively large number of species in the Gymnodiniidae distinguished by rose-red pigment. These are found in *Gymnodinium, Gyrodinium,* as well as in *Pouchetia.*

It falls within the subgenus *Glyphodinium,* being one of the least specialized members of that group, as shown in the slight ventral excavation of the body. It is the only known member of this subgenus with a red color.

## **Cochlodinium schuetti** sp. nov.

Plate 1, figure 8; text figure HH, 2

*Gymnodinium helix* Schütt (1895), in part, pl. 24, fig. $77_6$.

Diagnosis.—A medium sized species with rotund ellipsoidal body, its length 1.47 transdiameters; girdle a descending left spiral of 1.5 turns, displaced 0.52 transdiameter; sulcus with torsion of 0.5 turn; color, pale greenish yellow. Length, 59$\mu$. Pacific off La Jolla, California, July.

Description.—The body is rotund ellipsoidal in shape with broad apices, nearly circular in cross-section, its length 1.47 transdiameters at the widest part. The epicone and hypocone are subequal in size, though the total length of the former is slightly greater than the length of the latter. The epicone is subhemispherical in shape with broad apex. It has a length from the proximal and distal ends of the girdle of 0.38 and 0.75 respectively of the total length of the body. The hypocone is somewhat broader than the epicone, subtruncate posteriorly with the antapex indented by the sulcal notch.

The girdle is a descending left spiral of 1.5 turns and a displacement of 0.52 transdiameter. The distance of its proximal and distal ends from the apex is about 0.38 and 0.75 respectively of the total length of the body. The first 0.5 transdiameter of its course is deflected anteriorly at an angle of about 30°, gradually changing to a transverse direction on the left side, turning posteriorly on the dorsal face and again flattening to a transverse plane at its distal end. The furrow has a width of about 0.05 transdiameter and is deeply impressed with rounded, overhanging borders.

The sulcus may invade the epicone in a shallow loop which soon fades out or it may stop at its proximal junction with the girdle. Its width is somewhat less than that of the girdle in the intercingular area, expanding greatly posteriorly and forming a wide, rather shallow sulcal notch at the antapex. It is deeply constricted in the intercingular area, resulting in a lobed appearance of the ventral surface. The anterior and posterior flagellar pores are located at the anterior and posterior junctions of the girdle and sulcus respectively.

The nucleus is an ellipsoidal body filled with fine, moniliform chromatin strands following its longer axis. It is located in the posterocentral part of the body near the dorsal surface. Its major and minor axes are about 0.57 and 0.4 transdiameter respectively.

Pusules may be present at either or both pores. In the individual figured the two pusules were connected by a long slender canal, forming a tubular connection between the two pores. The cytoplasm is very clear and transparent with numerous blue-green droplets scattered through the peripheral zone. The anterior portion of the body was occupied by a large food mass sea-foam yellow in color. The color of the organism is a diffused pale greenish yellow. A large, thin-walled, hyaline cyst enclosed each of the individuals observed.

Dimensions.—Length, 59–74$\mu$; transdiameter, 40–50$\mu$; axes of nucleus, 23$\mu$ and 16$\mu$.

Occurrence.—Two individuals were taken July 20, 1917, 6 miles off La Jolla, California, with a No. 25 silk net, in a haul from 80 meters to the surface and in a surface temperature of 21° C.

Synonymy.—Schütt (1895) figured, as *Gymnodinium helix* Pouchet, two distinct forms. The first of these, shown in his figures $77_{1-5}$, plate 24, is evidently Pouchet's species. His figure $77_6$, however, differs from the others in the shape of the body, amount of torsion, and the posterior arrangement of girdle and

sulcus in their relation to the twisted posterior portion of the body. Both of these forms we have found in the plankton at La Jolla and have no difficulty in separating them. We therefore propose to separate his figure $77_6$ as a new species, *C. schuetti*. The elongate nucleus in Schütt's figure is evidently that of a predivision stage.

COMPARISONS.—This species belongs with the subgenus *Glyphodinium* and lies midway between *C. geminatum* (fig. GG, 1) and *C. vinctum* (fig. HH, 3), near the beginning of the series showing an increasing curvature and distortion of the body. The anteroposterior plane passing from apex to antapex is more ventrad in position in *C. schuetti* than in *C. geminatum* and less so than in *C. vinctum*, nearly equaling that of *C. rosaceum* (fig. HH, 4) in this respect.

## **Cochlodinium scintillans** sp. nov.

Plate 10, figure 113; text figure GG, 11

DIAGNOSIS.—A small species with subellipsoidal to biconical body, its length 1.4 transdiameters; girdle a descending left spiral of 1.5 turns, displaced 0.74 transdiameter; sulcus with apical loop and torsion of 0.5 turn; color, pearl grey with reddish tones. Length, 38$\mu$. Pacific off La Jolla, California, July.

DESCRIPTION.—The body is asymmetrically ellipsoidal approaching biconical, tapering at both apices, circular in cross-section, its length 1.4 transdiameters at the widest part, which is at the middle. The epicone is considerably larger than the hypocone, having a greater transdiameter as well as greater length. It has the shape of a cone of about 80° with the left side slightly elevated, deflecting the blunt apex somewhat to the right. It has a length on the left and right sides of 0.26 and 0.84 respectively of the total length of the body. The hypocone is subconical, its angle varying from 50° at the antapex to about 80° anteriorly, its sides slightly concave. It is narrower than the epicone with a more slender pointed antapex.

The girdle is a descending left spiral of 1.5 turns and a displacement of 0.74 transdiameter. The distance from the apex of the proximal and distal ends is about 0.26 and 0.84 respectively of the total length of the body. The furrow has a width of about 0.07 transdiameter, and is deeply impressed with smoothly rounded borders. The sulcus forms a loop on the epicone, terminating below the apex on the left side. After passing the anterior flagellar pore it is deflected to the left with a torsion of 0.5 transdiameter in the intercingular part of its course, beyond which it passes posteriorly to within a short distance of the antapex. Its width is about one-third that of the girdle and the furrow is relatively deeply impressed. The anterior and posterior pores are located at the anterior and posterior junctions of the girdle and sulcus respectively.

The nucleus is reniform in shape and filled with fine, parallel, moniliform chromatin strands following its longer axis. Its major and minor axes are about 0.51 and 0.29 transdiameters in length respectively.

The cytoplasm is finely granular with a number of greenish oil droplets scattered through it. In the posterior region was a large, spherical vacuole filled with a pink fluid. Below this was a rounded body, orange rufous in color, and near the apex a smaller one of jasper red. The general color of the cytoplasm is pearl grey with tints of red showing through it. This form, like so many of the Gymnodinioidae, showed a striking play of color through the cytoplasm, which is almost impossible of analysis and still harder to reproduce adequately.

DIMENSIONS.—Length, 38$\mu$; transdiameter, 27$\mu$; axes of nucleus, 15$\mu$ and 8$\mu$.

OCCURRENCE.—This was taken July 17, 1917, with a No. 25 silk net, 5 miles off La Jolla, California, in a surface haul and in a surface temperature of 20° C. A second individual was observed July 27 in a haul 4 miles off La Jolla, from 80 meters to the surface and in a surface temperature of 21°4 C.

COMPARISONS.—This species lies on the borderline between *Cochlodinium* and *Gyrodinium*, more nearly approaching the latter than perhaps any other species of this genus. It is the only biconical species in the genus. It belongs in the *C. miniatum* group of the subgenus *Cochlodinium*.

## **Cochlodinium strangulatum** Schütt

Text figure GG, 8

*Gymnodinium strangulatum* Schütt (1895), pl. 22, fig. 72.
*Cochlodinium strangulatum,* Schütt (1896), pl. 5, fig. 7.
*C. strangulatum,* Lemmermann (1899), p. 360.
*C. strangulatum,* Cavers (1913), pp. 182, 183, fig. $9_{15-16}$.

DIAGNOSIS.—A large species with ellipsoidal body, its length 1.8 transdiameters, girdle a descending left spiral of 1.6–1.75 turns, displaced 1.04 transdiameters; sulcus with apical and antapical loops and torsion of 0.8 turn; surface striate. Length, 198$\mu$. Atlantic (?) or Bay of Naples.

DESCRIPTION.—The body is robust, irregularly ellipsoidal with the one face forming an almost straight line, the other surface convex. The apices are broadly rounded. The epicone and hypocone are subequal. The epicone has a length above the proximal part of the girdle of 0.22 and from its distal extremity of 0.81 respectively of the total length of the body. It is subhemispherical in outline, convex ventrally, slightly so dorsally, with a broad, blunt apex excentrically placed towards the ventral side. It expands below the anterior flagellar pore region to nearly 1.4 of its width at that point, the expansion being entirely on the dorsal side. The hypocone is somewhat broader than the epicone. Its sides are rounded with a distinctly acuminate antapex which is ventrad from the midplane of the body.

The girdle joins the proximal end of the sulcus at about 0.22 of the total length of the body from the apex. It follows a descending left spiral course which makes 1.6–1.75 turns before joining the distal end of the sulcus at about 0.18 of the total length of the body from the antapex. It is relatively wide and deeply impressed with smooth, rounded borders. The position of the flagellar pores was not indicated in Schütt's figures.

The sulcus invades the epicone as a wide loop, terminating near the apex on the dextrodorsal surface. Posteriorly it follows a descending spiral course which makes about 0.8 turn in reaching its posterior junction with the girdle, beyond which it invades the hypocone in a curved line which terminates at the sinistrodorsal side of the antapex. It is broad and deeply imbedded, with high rounded borders.

The nucleus is spheroidal, and is located slightly posterior to the central part of the body. It shows two clearly differentiated regions, a peripheral clear zone and an inner portion. Its axis is about 0.4 transdiameter in length.

The cytoplasm is alveolar with numerous small spherules in the peripheral region overlying large alveoli. A globular pusule in the anterior region is connected with the anterior flagellar pore, presumably, by a long slender canal. The color of the organism was not noted. The

surface is minutely striate with closely set, equidistant striae, approximately equal in number on both epicone and hypocone and apparently about 60 across one face. In his figure 72, plate 22, Schütt (1895) shows a portion of an individual fixed with Flemming's solution and stained with haemotoxylin, from the posterior end of which stream long, pseudopodia-like strands of protoplasm. These did not appear in the living animal, but required staining to make them visible. They apparently have no definite place of origin and are probably artifacts, such as are frequently found in stained material.

DIMENSIONS.—Length, 198μ; transdiameter, 110μ; axis of nucleus, 54μ.

OCCURRENCE.—Figured by Schütt (1895) from material collected by the Plankton Expedition, presumably from the Bay of Naples or the Atlantic.

SYNONYMY.—This species was first described by Schütt (1895) as *Gymnodinium strangulatum*, and later (1896) changed by him to *Cochlodinium* as the type and only species of the genus when described. It is also the type species of the subgenus *Cochlodinium*.

COMPARISONS.—This is one of the largest species in the genus, being exceeded in size by only one species, *C. minatum*. It shares with this species the peculiarity of having a perinuclear, hyaline zone, as well as a striate surface, but differs from it in the absence of red pigment, shape of the body, and in having a hemispherical instead of a pointed apex. The species is otherwise quite isolated in the genus.

## **Cochlodinium turbineum** sp. nov.

Plate 9, figure 99; text figure GG, 9

DIAGNOSIS.—This is a minute species with broad, obovoidal body, its length 1.04 transdiameters; girdle a descending left spiral of 1.5 turns, displaced 0.56 transdiameter; sulcus with short apical loop and total torsion of 0.5 turn; color, yellowish green. Length, 26μ. Pacific off La Jolla, California, July, August.

DESCRIPTION.—The body is broadly obovoidal in outline, circular in cross-section, its length 1.04 transdiameters at the widest part about the middle of the body. The anterior part of the body is rotund, tapering posteriorly with the ventral face deeply constricted by the intercingular sulcus. The epicone greatly exceeds the hypocone in size, its length and transdiameter being greater. It is broadly rounded anteriorly with a length from the proximal and distal ends of the girdle of 0.31 and 0.88 respectively of the total length of the body. Its distal portion becomes drawn out to a slender point. The length of the hypocone posterior to the distal junction of the girdle and sulcus is about 0.05 of the total length of the body. The antapex is notched by the distal end of the sulcus.

The distance of the proximal and distal ends of the girdle from the apex is about 0.31 and 0.88 respectively of the total length of the body. In the first 0.8 transdiameter of its course the rotundity of the body throws it somewhat anteriorly, beyond which it turns posteriorly at an angle of 30° to 40° with the transverse plane on the left side of the body, traversing the right in a nearly transverse direction with another short posterior deflection to meet the sulcus. The furrow has a width of about 0.05 transdiameter and is deeply impressed. The anterior flagellar pore is located at the anterior junction of the girdle and sulcus and the posterior pore at the posterior junction.

The sulcus forms a short loop on the epicone, ending below the apex. Posterior to the anterior pore it takes a descending left course which makes 0.5 turn in reaching the antapex. It is narrow and deeply impressed with high-rolling borders. This with the girdle throws the ventral surface into a series of three rounded lobes.

The nucleus is large, ellipsoidal and placed slightly anterior to the central portion of the body. Fine, moniliform parallel chromatin strands traverse a course obliquely across its major axis. Its major and minor axes are 0.6 and 0.48 transdiameter in length respectively.

The cytoplasm is very clear and transparent with but few inclusions. Near the periphery are a number of refractive spherules and blue-green oil droplets. A food mass, yellow ochre in color, was found in the center of the body adjacent to the nucleus. The color is mingled yellow green and pearl grey.

Dimensions.—Length, 26μ; transdiameter, 25μ; axes of nucleus, 15μ and 12μ.

Occurrence.—A single individual was taken July 25, 1917, with a No. 25 net, 11 miles off La Jolla, California, in a haul from 80 meters to the surface and in a surface temperature of 21.8 C. Two individuals were taken August 8 in a haul 4 miles off La Jolla, from 80 meters to the surface and in a surface temperature of 22°5 C.

Comparisons.—This is the shortest and the smallest species in the genus *Cochlodinium,* and is most contracted posteriorly. Its rotundity, however, makes it nearly equal in size to *C. pulchellum* sp. nov. (fig. HH, 16), the latter having a greater length but about half its width. It belongs in *C. miniatum* group of the subgenus *Cochlodinium.*

## **Cochlodinium vinctum** sp. nov.

Plate 2, figure 15; text figure HH, 3

Diagnosis.—Medium sized species; body asymmetrically ovoidal or rotund, dorsally arched, length 1.4 transdiameters, girdle a descending left spiral of 1.50–1.65 turns, displaced 0.57–0.62 total length, sulcus with anterior and posterior loops. torsion 0.50–0.65 turns; plasma very clear, pale glaucous blue, sometimes tinged with yellow. Length, 50–75μ. Pacific off La Jolla, California, July, August.

Description.—The body is asymmetrically ovoidal to rotund in shape, according to the view. The more rotund forms may also owe their breadth in part to the great mass of cell inclusions present in such individuals. The anterior end is often a trifle broader and rounded, the posterior slightly narrower and also rounded, and the spiral ventral face deeply channeled and somewhat flattened, while the dorsal is arched, in the extreme condition almost hemispherical. The epicone and hypocone are subequal. The epicone has a length at the proximal and distal ends of the girdle of 0.18 and 0.65 respectively of the total length of the body. Its apex is subhemispherical with the flatter slope on the right side. The hypocone has a length at the proximal and distal ends of the girdle of 0.82 and 0.35, total length of the body. The antapex is subhemispherical with the flatter slope at the morphological right side of the sulcus. It is sometimes notched by the end of the sulcus.

The girdle joins the sulcus anteriorly at 0.18 of the total length of the body from the apex. It forms a descending left spiral of 1.6 turns, displaced about 0.57–0.62 diameter. It is deeply impressed, especially on the left side, forming with the sulcus a series of deep lobes on the

sinistroventral face of the body. It is less deeply impressed on the dextrodorsal surface. Its width is 0.08 transdiameter. The anterior flagellar pore opens at the anterior junction of the girdle and sulcus, the posterior pore at the posterior junction.

The sulcus invades the epicone in a short, curved extension which terminates near the apex. It passes posteriorly in the hollow of a very deep trough, making 0.50–0.65 turn before meeting the distal end of the girdle. Beyond the distal junction it widens to about twice its width above, and terminates on the left side of the median line at or near the postmargin, sometimes with a slight sulcal notch. Its total length anteroposteriorly is about 0.9 of that of the body.

The nucleus is spheroidal to ellipsoidal and located in the posterior half of the body. About ten moniliform chromatin strands traverse it spirally about its main axis. Its axes vary in length from 0.40 and 0.32 to 0.5 and 0.3 transdiameter respectively.

A large sacklike pusule opens distally into each flagellar pore. In one individual their proximal ends were connected, forming a complete channel between the two pores. The pusules are filled with a pale pinkish fluid. The cytoplasm is exceedingly clear and transparent, with no granular structure discernible. It usually contains from one to several food masses of ochraceous or greenish color. In the anterodextral part of the body is a large reniform, greenish or oil-yellow vacuolated body which seems to be a food mass. Every individual observed thereafter, however, contained this same body in about the same location. Its length is 0.80 to 0.85 transdiameter and its diameter about half its length. Its periphery is wholly covered with small, highly refractive spherules resembling oil drops of uniform size, arranged with considerable regularity. Its center contains an elongated pinkish vacuole, and in one instance what appears to be a nucleus of the dinoflagellate type is indicative of cannibalistic tendencies. No striations or other markings could be detected on its surface. The color is a pale glaucous blue. In the peripheral zone were a number of greenish spherules, probably oil droplets, and in one individual there was a peripheral zone of short radial rhabdosomes, faintly tinged with orange or yellow near the apices in some individuals.

DIMENSIONS.—Length, 50–75$\mu$; transdiameter, 36–63$\mu$; diameter of nucleus, 17$\mu$, or with a major and minor axes of 19–30$\mu$ and 15–19$\mu$ respectively.

OCCURRENCE.—The first individual was taken July 9, 1917, with a No. 25 silk net, 4 miles off La Jolla, California, in a haul from 80 meters to the surface, in a surface temperature of 19°8 C. On July 11 a second individual was taken under similar conditions in a surface temperature of 20°2 C. On July 20 it was again taken in a haul made 6 miles offshore, in a similar haul in a surface temperature of 21° C. A fourth individual was taken on August 10 in a haul from 50 meters to the surface, one mile offshore, in a surface temperature of 22°5 C.

ACTIVITIES.—When first placed under the cover glass this species is exceedingly active, incessantly on the move, circling mainly in close clockwise spirals only several lengths of the body in diameter. In about thirty to seventy minutes it slows down, rounds up, and undergoes cytolysis. It is prone to fasten itself to the slide by the anterior end, presumably the region of the anterior junction of the girdle and sulcus. It often circles for a long time without rotation of the body on its axis.

COMPARISONS.—This species belongs to the *C. distortum* series in the subgenus *Glyphodinium*, and lies midway between *C. rosaceum* (fig. HH, 4) and *C. convolutum* (fig. HH, 5). Its ventral excavation is much less than in *C. cavatum* (fig. HH, 10), its torsion is greater and its displacement of girdle less,

9.59–9.62 as compared with 0.64. Its proportions are much stouter, its length being 1.4 transdiameters as compared with 2.25. It differs from *C. conspiratum* (fig. GG, 10) in being nearly twice as long, having 0.50–0.62 instead of 0.9 turn in the torsion of the sulcus, and in possessing a longitudinal instead of a transverse antapical loop.

The nature of the large vacuolated structure interpreted by us a food mass is problematical. In the number and regularity of the vacuoles it is unlike other food masses. There is, however, no such regularity in these structures as appears in the nuclei of *Amoebophrya* parasitic in *Sticholonche* (see Borgert, 1897), and there is no motion in the structure such as we have observed in this parasite in *Pouchetia*. The interpretation of the structure as a parasite thus appears to be excluded. The presence of the mass inside of a vacuole, and the concentration of vacuoles about it, suggest a food mass in a rapid phase of intracellular digestion. In case this is the correct interpretation, the similarity of the mass in size, location, and condition in all of the individuals can be explained only on the basis of the capture of the same type of food at about the same interval prior to observation on the part of all of the four individuals observed. This is a sufficient number of instances to suggest selective feeding on the part of the organism. The nature of the food could not be determined. Its shape and size do not agree with any known dinoflagellate. The presence of a nucleus recognizably of the dinoflagellate type in one instance indicates that the food may be one of the many small and as yet undescribed dinoflagellates which occur in the plankton.

### **Cochlodinium virescens** sp. nov.

Plate 9, figure 104; text figure HH, 11

Diagnosis.—A medium sized species with ellipsoidal, nearly symmetrical, deeply constricted body; its length 1.5 transdiameters; girdle a descending left spiral, displaced 0.8 transdiameter; sulcus with torsion of 0.9 turn; color, yellowish green. Length, 54μ. Pacific off La Jolla, California, July, August.

Description.—The body is ellipsoidal in outline with broad, rounded apices, nearly circular in cross-section, its length 1.5 transdiameters at the widest part at the middle. When first confined under the cover glass the body is generally deeply constricted by the sulcus and girdle, but still subsymmetrical, rounding out after being kept for some time under the microscope. The epicone and hypocone are subequal in size. The epicone is subhemispherical in shape, sometimes slightly flattened at the apex or notched at the left side by the anterior end of the sulcus. Its length from the proximal and distal ends of the girdle is 0.2 and 0.74 respectively of the total length of the body. Its distal portion forms a wide band which makes about 0.9 turn around the body. The hypocone is subhemispherical in shape with broadly rounded or more or less deeply notched antapex.

The girdle is a descending left spiral with a distance from the apex at its proximal and distal ends of 0.2 and 0.74 respectively of the total length of the body, and its displacement is 0.8 transdiameter. The major part of its posterior descent takes place in the middle third of

its course, its course proximally and distally having a nearly transverse direction. The furrow has a width of about 0.05 transdiameter, but is obscured throughout most of its course by the rotundity of its borders. It is deeply impressed, often constricting the body to about 0.63 transdiameter, and, with the sulcus, throwing the right and left sides of the body into four nearly alternating rounded lobes.

The sulcus usually invades the epicone in an apical loop that may fade out before reaching the apex or may notch the left side below the apex. After passing the proximal end of the girdle it turns to the left in a descending spiral of about 0.9 turn, meeting the girdle distally about 0.24 of the total length of the body from the antapex. Beyond the distal junction it turns slightly towards the right, broadening and often notching the right side of the antapex. The anterior flagellar pore opens at the proximal junction of the girdle and sulcus, and the posterior pore somewhat below the distal one.

The nucleus is a large, spheroidal body filled with coarse, moniliform chromatin strands. It is located somewhat posterior to the midplane of the body, on the left side. Its axis is about 0.44 transdiameter in length.

In all the individuals of this species observed the pusules were united at their extremities, forming a long tubular canal between the two flagellar pores. The cytoplasm is clear and transparent, often with no trace of granulation. Food bodies are usually present as well as oil globules, refractive bodies and minute blue-green granules scattered through the peripheral zone. The color of the organism is a mixture of pearl grey and green, with a trace of orange peripherally, varying to light turtle green throughout.

DIMENSIONS.—Length, 52$\mu$; transdiameter, 36–45$\mu$; axis of nucleus, 15–24$\mu$.

OCCURRENCE.—The first specimen observed was taken July 11, 1917, with a No. 25 net, 4 miles off La Jolla, California, in a haul from 80 meters to the surface in a surface temperature of 19°7 C. It was later observed in most of the hauls made from August 3 to 20, 0.75 to 6.5 miles offshore, from 60 to 80 meters depth and in surface temperatures varying from 19°7 C to 22°4 C.

COMPARISONS.—This species is distinct in the genus *Cochlodinium* in the amount of constriction of the body by the girdle and sulcus, the constriction occurring throughout the entire length of both furrows, with the greatest depression along the sulcus. The latter feature is common in the species of the subgenus *Glyphodinium*, without, however, showing a corresponding constriction of the girdle.

*Cochlodinium virescens* belongs in the *C. citron* group of the subgenus *Cochlodinium*, and lies midway between *C. lebourae* (fig. HH, 7) and *C. radiatum* (fig. GG, 12).

## **Cochlodinium volutum** sp. nov.

Plate 10, figure 108; text figure GG, 1

DIAGNOSIS.—A medium sized species with obovoidal body, its length 1.46 transdiameters; girdle a descending left spiral of 1.5 turns, displaced 0.82 transdiameter; sulcus with torsion of 0.5 turn; surface coarsely striate; color, yellow green. Length, 60$\mu$. Pacific off La Jolla, California, August.

DESCRIPTION.—The body is obovoidal in shape, nearly circular in cross-section, broadly rounded anteriorly and contracting posteriorly, its length 1.46 transdiameters at the widest

part in the anterior part of the hypocone. The dorsal surface is more convex than the ventral, thus placing both apices slightly ventrad of the median frontal plane of the body. The hypocone exceeds the epicone in size. The epicone is broadly rounded, less than a hemisphere, with a length from the proximal and distal ends of the girdle of 0.19 and 0.82 respectively of the total length of the body. On the dorsal and right sides of the body the basal portion forms a flaring border to the girdle, with less prominence elsewhere. The hypocone is conical in shape, with an angle of about 45°. It is narrower distally than the epicone with rounded antapex. Anteriorly it forms a shelflike border to the girdle.

The proximal and distal ends of the girdle join the sulcus at a distance from the apex of 0.19 and 0.82 respectively of the total length of the body. It sweeps around the body in a descending left spiral of 1.5 turns with a displacement of 0.82 transdiameter. The first transdiameter of its course is nearly transverse beyond which it turns posteriorly at a gradually steepening angle which becomes about 35° for the last 0.5 of its course. The furrow has a width of about 0.08 transdiameter, slightly narrower anteriorly, and is deeply impressed with borders raised somewhat above the surrounding surface.

The sulcus invades the epicone to within a short distance of the apex. After passing the proximal end of the girdle it is deflected to the left, and continues posteriorly in a spiral course to near the antapex, its torsion about 0.5 turn. It is rather shallow with smooth borders. The anterior and posterior flagellar pores open at the anterior and posterior junctions respectively of the girdle and sulcus.

The nucleus is a large ellipsoidal body, filled with fine, parallel, moniliform chromatin strands which follow its long axis. It is located in the anterocentral part of the body. Its major and minor axes are 0.46 and 0.31 transdiameter respectively.

The cytoplasm is very clear and transparent, and contains numerous blue-green oil globules of varying sizes. A small, club-shaped pusule opens into the posterior flagellar pore, a larger, sacklike one with a long, slender, curved diverticulum extending dorsad, opening into the anterior pore. The surface is striate with longitudinal blue-green lines extending from the girdle to the apices. The number of lines on the epicone exceeds the number on the hypocone by about 0.2. The general color of the organism is yellowish green diffused throughout the cytoplasm.

Dimensions.—Length, 60$\mu$; transdiameter, 41$\mu$; axes of nucleus, 19$\mu$ and 13$\mu$.

Occurrence.—Two individuals were taken August 10, 1917, with a No. 25 silk net, 1 mile off La Jolla, California, in a haul 50 meters to the surface, in a surface temperature of about 21° C.

Comparisons.—In the type of spiral the girdle of *C. volutum* resembles somewhat that of *C. conspiratum* (fig. GG, 10), being slightly more regular in its course. In shape of body and apices it is close to *C. scintillans* sp. nov. (fig. GG, 11), but has striae on its surface. It belongs to the *C. miniatum* group of the subgenus *Cochlodinium*, and shares with *C. miniatum* the distinction of a *Gyrodinium* type of striate surface.

CHAPTER XV

## GYMNODINIIDAE: TORODINIUM

### **TORODINIUM** gen. nov.

Text figure II

*Gymnodinium*, Pouchet (1885*a*), in part, p. 67, pl. 4, fig. 29.
*Gymnodinium*, Lemmermann (1899), in part, p. 358.
*Gymnodinium*, Schütt (1895), in part, pl. 165, pl. 23, fig. $74_{1-10}$.
*Gymnodinium*, Paulsen (1908), in part, pp. 97, 98, fig. 132.

#### Diagnosis

Body elongate, epicone several times the length of the hypocone in length, girdle and hypocone forming an augur-shaped cone at the antapex; girdle forms a descending left spiral of slight displacement; sulcus with very long apical loop with torsion of about 0.5 turn posteriorly and straight antero-longitudinally, running most of the length of the body nearly to the apex; nucleus faint, greatly elongated; rhabdosomes linear, sinistral, longitudinal; marine, eupelagic. Two species; the type, *Torodinium teredo* (Pouchet), was described by Pouchet (1885*a*, p. 67, pl. 4, fig. 29) as *Gymnodinium teredo*.

#### Description

The marked torsion of the sulcus, amounting to 0.5 turn, equivalent to that in the simplest species of *Cochlodinium* and without parallel elsewhere in *Gymnodinium*, serves to exclude *Gymnodinium teredo* from the genus in which Pouchet (1885*a*) described it, and in which all subsequent investigators have left it. In all species of *Cochlodinium*, as well as of *Gymnodinium* (except in *G. glaucum* Lebour), the anterior flagellar pore is at least premedian and never pushed back almost to the antapex, as in *T. teredo* (fig. II). In correlation with this posterior dislocation of this pore and the accompanying girdle in *Torodinium*, the sulcus stretches anteriorly almost to the apex, retaining 0.5 turn or more of the characteristic torsion of the apical loop, but exhibiting little or no torsion in its very much foreshortened intercingular and antapical portions. This unique arrangement of these fundamental organs,

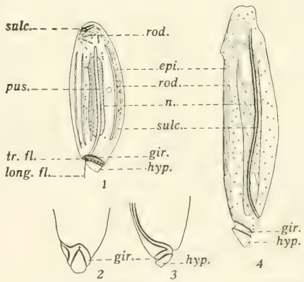


Fig. II. *Torodinium* gen. nov. 1. *Torodinium robustum* sp. nov. Left lateral view. 2. Ventral view of antapical region. 3. Right lateral view of antapical region of same figure. 4. *Torodinium teredo* (Pouchet). After Schütt (1896, pl. 23, fig. $74_{1}$). Abbreviations: *epi.*, epicone; *gir.*, girdle; *hyp.*, hypocone; *long. fl.*, longitudinal flagellum; *n.*, nucleus; *pus.*, pusule; *rod.*, rodlets or rhabdosomes; *sulc.*, sulcus; *tr. fl.*, transverse flagellum. × 500.

girdle and sulcus, compels the establishment of a separate genus to include this aberrant species. The first step in this divergence is to be found in the aberrant *Gymnodinium glaucum,* which forms a connecting link between the two genera.

The nucleus is conformable to the body in proportions and shape, being, in *T. teredo* (fig. II, 4), eight times as long as it is wide. It is exceptionally transparent and difficult to detect because of the delicacy of its membrane and transparency of the exceptionally coarse and ropelike, longitudinal, spirally twisted chromatin threads.

The marked asymmetry of the body is exhibited not only in the asymmetrical contour of the short hypocone but also in the grouping of the rhabdosomes which are linear in form and massed entirely on the left side of the body in four parallel rows and in a star near the apex. It is possible that these structures, which we designate as rhabdosomes, are in reality chromatophores.

## Comparisons

The structure of this genus is so unique and so far removed from other genera that its relations are in no case immediate. It is clear, however, that in the torsion of the sulcus it is nearer to *Cochlodinium* than to *Gymnodinium.* In its posterior location of the girdle it is unique and at the opposite extreme from *Erythropsis,* in which the girdle is far anterior with a compensating reduction of the epicone. The extreme reduction of the hypocone in *Torodinium* is without parallel among free-living Gymnodinioidae, except as foreshadowed in *Gymnodinium glaucum.*

It is also worthy of note that the cytoplasmic differentiations of pigmented rhabdosomes (or chromatophores?) are sinistral as is the ocellus of *Erythropsis,* but they are in the epicone instead of the hypocone as in the latter genus.

## Historical Discussion

The first species now included in this genus was described by Pouchet (1885*a*) as *Gymnodinium teredo.* Schütt (1895) found both species, but did not differentiate them, referring them both to *G. teredo.* We have found only the stouter of these two species, *Torodinium robustum,* in which we include the first two of Schütt's figures (1895, pl. 23, figs. $74_{1-2}$) of *G. teredo,* referring the remainder to the species to which he assigned them.

## Key to Species of **Torodinium**

Length less than 3.5 greatest transdiameters, sulcus with reversed terminal apical loop .................................................. **robustum** sp. nov.

Length more than 4 transdiameters, no loop in terminal part of the sulcus ...... **teredo** (Pouchet)

## **Torodinium robustum** sp. nov.

Plate 4, figure 49; text figure II, 1–3

*Gymnodinium teredo,* Schütt (1895), in part, pl. 23, figs. $74_{1-2}$. Figs. $74_{3-10}$ are *T. teredo* (Pouchet).

Diagnosis.—Medium sized species, elongated, fusiform, its length 2.8 to 3.2 transdiameters; epicone 0.83 to 0.85 total length; hypocone minute, conical, asymmetrical; girdle a descending left spiral, displaced slightly; sulcus with torsion of 0.4 turn proximally and 0.75 reversed turn in apical region. Length, 67$\mu$ to 75$\mu$. Atlantic or Bay of Naples; Pacific off La Jolla, California, July.

Description.—The body is elongate fusiform, with little taper, slightly fuller anteriorly, widest at the middle, its length 2.8–3.2 transdiameters measured at the widest part near the middle. The epicone greatly exceeds the hypocone, its length at the proximal end of the girdle 0.83–0.88 total length, while at the distal end it almost reaches the antapex, apex broadly rounded; hypocone reduced to a minute asymmetrical cone which with the girdle above it takes on the form of the tip of an augur (fig. II, 1–3, *hyp.*). Its length at the proximal end of the girdle is 0.12 to 0.15 of the total length, and its diameter 0.3 to 0.4 transdiameter. It is quite asymmetrical with its antapex towards the right (of the body) of the major axis when viewed ventrally, that is, with the anterior pore midventral. Its ventral slope is about twice as long as the dorsal. It forms a lopsided cone of 70°–90°, according to the view or degree of contraction and its antapex is pointed.

The girdle is a descending left spiral slackening distally, displaced about twice the width of its furrow, its distal end merging directly with the distal end of the sulcus (fig. II, 1–3, *gir.*). The furrow is deeply impressed with prominent, overhanging lips. The diameter of the body in the oblique girdle is only about 0.35 transdiameter. The sulcus runs almost from apex to antapex. Assuming for purposes of description that the location of the anterior flagellar pore establishes the planes of orientation of the body as a whole we may define the course of the sulcus as follows. It begins very near the anterior end with a reversed loop of nearly 0.75 turn, that is, running from the left side of the body around ventrally to its right instead of the usual spiral course seen in the torsion of the sulcus. This loop is deflected posteriorly 10°–15° below the horizontal, increasing posteriorly to within less than a transdiameter of the anterior end, where it has turned to a posterior direction, which it then pursues longitudinally a little to the right of the middorsal line. At 0.5 transdiameter from the antapex it turns in the customary descending left spiral for 0.4 turn at 25° below the horizontal to its junction with the girdle. Its course below this point is a short expanded area on the ventral face of the button-like hypocone. The transverse flagellum encircles the body and the stout posterior flagellum is one transdiameter in length. Both arise close together near the proximal end of the girdle.

The nucleus is an elongated rod with rounded ends, 0.5 of the length of the body in length and slightly wider posteriorly. Its length is six times its middiameter. It is traversed by about ten coarse, moniliform chromatin threads which form a steep spiral about its main axis. The nuclear membrane is very faint and the nucleus remarkably difficult to discern in life. From the anterior flagellar pore there runs anteriorly at the left of the nucleus a slender canal, the anterior pusule. No posterior pusule was found. On the left side of the body are four continuous linear peripheral "chromatophores" or rhabdosomes, which were a pale oural green in our specimens. Schütt (1895) figures them as of the same pale ochre as those of his other figures of *G. teredo.* They are 0.65 of the total length of the body in length, equidistant and somewhat unequal in length. Grouped about a central oil globule in the sinistroventral part of the apical region is a partial chromatophore (?) star of eight or nine rays grouped mainly

on the anterior arc of a complete circle. Scattered through the cytoplasm are numerous highly refractive spherules filled with a glaucous green fluid. Schütt (1895) figures a layer of peripheral radial rhabosomes in regions where there are no chromatophores (?). There is no evidence that this organism is holozoic, neither is the color of the "chromatophores" or rhabdosomes conclusive of holophytic nutrition.

There are no striae on the surface. The general color of the plasma is a pale veronese green. Rhabdosomes or chromatophores and nucleus alike round up, as cytolysis approaches, and the body itself also foreshortens and rounds up till its transdiameter is half its length.

DIMENSIONS.—Length, 65–75 (83)$\mu$; transdiameter at widest part, 21–23 (25)$\mu$; dorsoventral diameter in oblique girdle, 6–8 (8)$\mu$; axes of nucleus, 5$\mu$ and 32$\mu$. Dimensions of Schütt's figures (1895, pl. 23, figs. $74_{1-2}$) are given in parentheses.

OCCURRENCE.—This species was recorded in the plankton taken 4 to 11 miles off La Jolla, California, in July and August, 1917, in hauls taken from depth of 80 to 20 meters to the surface in surface temperatures of 18°8 C to 22°5 C. It was not recorded in all the catches, but in considerably more than half of them. As high as fifteen individuals were noted in one collection. It was never noted in the plankton taken daily at four-hour intervals off the pier at the Biological Station.

It was also recorded July 3, 1906, in a haul 2.75 miles off La Jolla from 155 meters to the surface in a surface temperature of 20°4 C.

Schütt (1895) figures it presumably from the Bay of Naples or from the collections of the Plankton Expedition in the Atlantic. The records of *Gymnodinium teredo* made by Schröder (1900) at Naples may exclude this species since he cites only Pouchet's (1885*a*) figure, which is *Torodinium teredo*. On the other hand Lebour (1917*b*) notes a "variety of shapes" in the material of *G. teredo* at Plymouth. This suggests the occurrence of this species in her material.

ACTIVITIES.—This is an exceeding active organism, darting about in long trajectories with little curvature. Its incessant rotation makes observation difficult. When quiescent it usually lies with the left side uppermost and is not easily dislodged, suggesting some adhesive function of the sulcus which on the applied face may be locally active in taking hold on the substrate. The antapical region is particularly difficult to interpret owing in part it seems to some mobility of the borders of the girdle and sulcus.

COMPARISONS.—This species differs from *T. teredo* in its stouter body and shorter main axis, 75$\mu$ as against 110$\mu$. The main distinction, however, appears to lie in its possession of a reversed terminal anterior loop of 0.75 turn of the sulcus. This is wholly lacking in *T. teredo* (fig. II, 4). The turn of the sulcus immediately above the girdle is a trifle shorter (0.4) in *T. robustum* than in *T. teredo* (0.5). The more greenish tone noted in the plasma in our specimens and in the so-called chromatophores as compared with the ochraceous tones of Schütt's (1895) may be wholly a metabolic phenomenon and not a specific distinction. Our observations lead us to the conclusion that *T. robustum* and *T. teredo* are not phases due to contraction or metabolism of the same species.

## **Torodinium teredo** (Pouchet)

Text figure II, 4

*Gymnodinium teredo* Pouchet (1885*a*), pp. 67, 82, 88, pl. 4, fig. 29.
*G. teredo,* Schütt (1895), in part, pp. 5, 6, 65, 71, 109, 115, 117, pl. 23, figs. $74_{3-10}$. Figs. $74_{1-2}$ are *Torodinium robustum* nom. sp. nov.
*G. teredo,* Lemmermann (1899), p. 358.
*G. teredo,* Schröder (1900), p. 13.
*G. teredo,* Karsten (1907), p. 307.
*G. teredo,* Paulsen (1908), in part, pp. 97–98, fig. 132.
*G. teredo,* Lebour (1917*b*), in part (?), pp. 188, 197.

Diagnosis.—Medium sized species, body elongate, subfusiform, length 4.3–5 transdiameters; epicone forms 0.88–0.91 total length; girdle forms proximally a descending left spiral, without overlap, displaced less than 1.5 furrow's width; sulcus with torsion of 0.5 turn adjacent to the girdle, no loop at apex. Length, 100–113$\mu$. Atlantic, Pacific, and Indian oceans, Plymouth Sound, Mediterranean.

Description.—The body is elongate asymmetrically subfusiform, left side (of sulcus) more convex, widest near the middle, length 4.3–5 transdiameters measured at the widest part; epicone very greatly exceeds the hypocone, forming 0.88–0.91 total length of the body; the hypocone is subconical with an angle of 50°, with its axis ventral to the main axis and the dorsal slope nearly twice the length of the ventral, with pointed antapex. In combination with the girdle it forms a single turn of a descending left spiral, with a total displacement dorsally of about 1.5 widths of the furrow. The proximal 0.5 turn on the left side descends 20° from the horizontal to the middorsal line, but ascends again in the distal part with the result that the ventral face of the hypocone is longer than the dorsal (fig. II, 4). There is no overlap. The furrow has an overhanging anterior lip and is deeply impressed. Its width is about 0.12 transdiameter at the widest part of the body.

The sulcus originates anteriorly within a short distance of the apex, runs longitudinally posteriorly to within 1 transdiameter of the antapex, turns in a descending left spiral for 0.5 turn at about 45° to its junction with the girdle on the opposite side. It is not distinguishable beyond this point. It has no reversed loop in the anterior end of the body. The flagellar pore lies near the junction of girdle and sulcus.

The nucleus is elongated cylindrical with rounded ends. Its major and minor axes are respectively 3 and 0.45 transdiameters in length. It is traversed diagonally by 8–10 vaguely outlined spiral chromatin strands and its boundaries are indistinct. A longitudinal pusule, opening posteriorly at the flagellar pore, runs anteriorly nearly to the apex. It may be broken up into a line of separated vacuoles (Schütt, 1895). Refractive fatty spherules of varying sizes are clustered near the apex and along the right side and an axial plastid containing what Schütt (1895) has called $\beta$-oil may be located in the anterior half of the epicone. Ochraceous chromatophores or rhabdosomes arranged in four longitudinal rows of rods from 0.5 to 1 transdiameter in length and about 0.1 in diameter are found on the left side for the middle 0.7 of the total length of the body. Several additional stouter chromatophores or rhabdosomes as radii are found above the four rows near the apex. They are clustered about a central oil spherule.

The plasma is almost colorless and shows no peripheral striae.

Dimensions.—Length, 100–113$\mu$; transdiameter at widest part of the body, 23–26$\mu$; axes of nucleus, 75$\mu$ and 10$\mu$.

Occurrence.—Occasional in the plankton taken off La Jolla, California, in July and August, 1917, in hauls from 80 meters to the surface in surface temperature of 19° C to 21°5 C. Reported by Pouchet (1885*a*) from the Atlantic at Concarneau and by Miss Lebour (1917*b*) from Plymouth Sound, England, where it was abundant in July and August, and rarely even into the winter months, during which it was the only representative of the Gymnodinioidae found. The extreme variability noted by Miss Lebour may be due to the inclusion of *T. robustum* in this species. Schröder (1900) found it in July and August in the plankton of the Bay of Naples; and Karsten (1907) records it in one haul of the Valdivia Expedition, made from 100 meters to the surface near the center of the Indian Ocean in March. It thus appears to be a eupelagic species, probably of wide distribution in tropical and warm temperate seas.

Comparisons.—This is the slenderest species not only of *Torodinium* but likewise of all of the free-living Gymnodinioidae. The shortening of the transverse flagellum and of the girdle in which it lies has extended to such a degree that the transdiameter of the body in this region is little more than 0.35 of that of the widest part of the body, a region in which the girdle is normally located in most Gymnodinioidae.

Synonymy.—This species was described as *Gymnodinium teredo* by Pouchet (1885*a*), and has been retained in that genus by all subsequent investigators who have dealt with it. Schütt (1895) did not separate it from *T. robustum*, which he includes in his figures of *T. teredo*. This confusion appears to have been continued by Lebour (1917*b*), and possibly others.

CHAPTER XVI

# POLYKRIKIDAE: POLYKRIKOS

## Family 3. POLYKRIKIDAE fam. nov.

Diagnosis.—Gymnodinioidae with a permanent colonial organization, 2, 4, or 8 zooids in chain, each zooid having a *Gymnodinium* type of structure; girdle a descending left spiral of one turn; sulcus extending from apex to antapex; ocellus and tentacle lacking; plasma colored without pigment; nematocysts present. Marine, eupelagic and neritic, and from warm temperate waters. One genus.

### **POLYKRIKOS** Bütschli

Text figure F

*Polykrikos* Bütschli (1873), pp. 673–676, pl. 26, fig. 22; (1885), pp. 1011, 1012, pl. 55, fig. 8.
*Polykrikos,* Saville-Kent (1880–82), pp. 858, 860.
*Polykrikos,* Bergh (1881*b*), pp. 255–259, pl. 16, fig. 72.
*Polykrikos,* Delage and Hèrouard (1896), p. 386, fig. 679.
*Polykrikos,* Calkins (1901), p. 140.
*Polykrikos,* Lang (1901), p. 23.
*Polykrikos,* Hartog (1906), pp. 110, 131, 132.
*Polykrikos,* Kofoid (1907*b*), pp. 291–293, fig. 1.
*Polykrikos,* Paulsen (1908), pp. 106, 107, fig. 149.
*Polykrikos,* Poche (1913), p. 162.
*Polykrikos,* Chatton (1914*c*), pp. 157–194, figs. 1–13; pl. 9, figs. 1–14.
*Polykrikos,* West (1916), pp. 54, 79, fig. 39.

#### Diagnosis

Polykrikidae of 2, 4, or 8 zooids in chain, each zooid with a *Gymnodinium* type of structure, girdle a descending left spiral of 1 turn; sulcus extending the whole length of the body and continuous with that of the adjacent zooids, each zooid having the same orientation. Number of nuclei is usually less than that of the zooids, generally in a ratio of 1 to 2. Nematocysts present; surface of hypocone ribbed or smooth; holozoic nutrition. Plasma colored, without pigment. Length of chain of 4 zooids, 215$\mu$. Marine, eupelagic and neritic, and from warm temperate waters. Two species.

#### Organology

The individual zooids of *Polykrikos* differ but little from many species of the genus *Gymnodinium*, their colonial habit and the presence of nematocysts alone separating them from that genus. The body of the colony as a whole is

elongate barrel-shaped, the extreme length reached in the eight-zooid stage being 4–5 transdiameters at the widest part near the middle. The girdle is usually transverse with its posterior displacement occurring at its distal extremity.

The body is without appreciable torsion, each zooid having the same orientation as its neighbor, with their sulci connected at their extremities and forming a continuous channel along the ventral face of the colony. The sulcus usually terminates near the right side of the apex of the proximal zooid and at the antapex of the distal one.

The nucleus of *Polykrikos* has the beaded chromatin strands characteristic of the Dinoflagellata generally and is without a distinct perinuclear zone. The number of nuclei in the colony is usually half the number of zooids.

The color of the cytoplasm of *Polykrikos* varies from a greenish tint, or almost colorless, to faint, diffuse rose, and is probably subject to considerable modifications through the food ingested by the organism. It is not improbable that the rosy tint results from feeding upon rose or red colored forms, like *Peridinium divergens* and *P. conicum*, usually abundant in the plankton with it. *Noctiluca scintillans*, feeding on the same plankton, exhibits a similar varying rosy tint in its color. The presence or absence of this color is one of the characters which Bergh (1881*b*) uses in separating his *Polykrikos auricularia* from Bütschli's species (1873), *P. schwartzi*, a distinction which is apparently not well grounded.

*Polykrikos* is holozoic in nutrition, as the abundance of individuals found with recognizable organisms in the cytoplasm indicates. These may include almost all the small organisms occurring in the plankton with it, both metazoan and protozoan.

The nematocysts of *Polykrikos* are found in all individuals without exception. They vary considerably in number and arrangement and have been observed to shift their position during the spasmodic plasmatic movements sometimes seen in the interior of the organism, and are often crowded to peripheral locations by the relatively large food masses sometimes ingested. They are not, when developed, fixed organs with definite locations, but may occur in any part of the body. Chatton (1914*c*) has demonstrated their origin from the serially arranged centrosomes at the right of the nuclei.

Division in *Polykrikos* is accomplished by the formation of new girdles between the already existing ones, followed by a division of the nuclei. A division of the colony is accomplished by a constriction of the body along the line of separation of the middle zooids, and may occur in four, eight, or sixteen zooid stages.

### Distribution

*Polykrikos* occurs along the western coast of Europe, as far north as Norway, in the Mediterranean, and along the coast of California, giving it a known distribution that is exceeded in its breadth by only a few species among the Gymnodinioidae. Its occurrence is thus confined largely to warm temperate

waters, or to the more northerly waters which receive warm currents, yet the significance of this fact is greatly modified by its seasonal distribution. Its occurrence in its more northerly range is quite as frequent in the colder as in the warmer months. Thus it has been found in the North Sea and the Skagerack from September to January (Aurivillius, 1896–98) and along the coast of Norway in November and December (Jörgensen, 1899).

*Polykrikos,* unlike most of the Gymnodiniidae, is fairly well able to withstand the destructive influences of fixing fluids, and is occasionally found in preserved material. In examinations of the plankton hauls made off San Diego for several years and covering every month of the year specimens of *Polykrikos* have been found only in the hauls made during June and July of different years. In the summer of 1917 it was present from June 26 to August 22, though never abundant. It has been found in San Francisco Bay in October and November.

## Historical Discussion

The history of *Polykrikos* has been a varied one, owing to its peculiar structure, which, in the earlier descriptions of it, was but imperfectly understood and served to obscure its relationships. The organism was first described by Ouljanin (1868) as a pelagic turbellarian larva and later by Bütschli (1873) as a ciliate infusorian, *Polykrikos schwartzi.* In 1881*b* Bergh referred it to the Cilioflagellata, added another species, *P. auricularia*, and figured cilia on the transverse furrows. Later Pouchet (1883, 1887) accepted this allocation, without, however, figuring the cilia. Bütschli (1885) in his monograph on the Dinoflagellata recognized the dinoflagellate character of this organism and omitted the cilia in his figures, substituting flagella therefor. He placed it in a separate family, Polydinidae. Schütt, both in his systematic monograph of the Peridiniales (1896) and in his report on the Peridiniales of the Plankton Expedition (1895), omitted all reference to the genus.

Delage and Hèrouard (1896) marked it off as a still more unusual form by creating for it the order Polydinida with this genus as its sole representative. Kofoid's (1907*b*) work on this puzzling organism served to clear up many of the obscure points in its structure with a resulting clearer elucidation of its relationships. He placed it in the family Gymnodinidae (=Gymnodiniidae) without further isolation unless that family should be broken up into subfamilies. A critical examination of an abundance of material also indicated that both Bütschli and Bergh were dealing with one and the same organism and not with two distinct species. Our later work on *Polykrikos* confirms these earlier observations (Kofoid, 1907*b*), and we therefore place Bergh's species as a synonym of Bütschli's *P. schwartzi.*

The form figured by Kofoid was afterward separated from *P. schwartzi* by Chatton (1914*c*), as *P. kofoidi.* The specific distinctions on which he based this separation are two in number, the first being the absence of nematocysts,

and the second the presence of distinct longitudinal striae, or furrows, on the hypocone of each zooid. The first distinction is not a valid one, since the nematocysts were intentionally omitted from the original drawing with most other internal structures. Each individual of this genus found in the waters of the San Diego region is provided with these distinctive organelles. The second distinction, namely, the surface markings on the hypocone (fig. F, 1), clearly marks this species off from *P. schwartzi*, which is also present in the waters of San Diego. In other respects these two species appear to be nearly identical, and the final critical discussion of their status awaits a reinvestigation of the Pacific species, if such it be.

### Key to Species of **Polykrikos**

1. Surface of hypocone of each zooid deeply ribbed, girdle displaced one-fifth length of body .... **kofoidi** Chatton
2. Surface of hypocone smooth, girdle without displacement .......... **schwartzi** Bütschli

### **Polykrikos kofoidi** Chatton

Plate 4, figure 47; text figure F, 1

*Polykrikos schwartzi*, Kofoid (1907*b*), in part, pp. 291–293, fig. 1.
*P. kofoidi* Chatton (1914*c*), p. 161.

Diagnosis.—This is a colonial form of 2.4, 8, or 16 individuals in chain, each individual rather small in size, its length about 0.43 transdiameter; girdle submedian, displaced 0.15 transdiameter; sulcus extending length of body; surface of hypocone ribbed; nematocysts present; color, greenish grey to rosy. Length of chain of 4 zooids, 110$\mu$. Pacific off La Jolla, California, June to August.

Description.—The individual zooids are small in size, rotund, nearly circular in cross-section, or slightly dorsoventrally depressed with a length of about 0.43 transdiameter. The epicone and hypocone are subequal in size with a tendency towards a slight decrease in the relative size of the epicone. The chain of two, four, or eight zooids presents a barrel-shaped appearance with broadly rounded apices, somewhat constricted at the girdles and the points of separation of the different zooids. The girdle of each zooid is submedian or slightly premedian in position. It follows a nearly transverse direction around the body with a slight posterior deflection of the distal end, resulting in a displacement of about 0.15 transdiameter. The furrow has a width of about 0.03 transdiameter and is deeply impressed, the excavation having a slight anterior extension, deeply undercutting the anterior border and gradually rounding out to the posterior one. The anterior lip is usually smooth and the posterior one often thrown into undulations similar to those on the surface of the hypocone.

The sulcus forms a continuous furrow on the ventral face of the chain of zooids, extending in a slightly sinuous line from near the apex of the first zooid to the antapex of the last one. Its width is about half that of the girdles, enlarging slightly at the points of union with the girdles and usually at place of union of the different zooids. At the antapex of the posterior zooïd its sides become widely deflected, forming a wide, shallow notch on the ventral face. The anterior flagellar pores open at the proximal junctions of the girdles and sulcus, the posterior

pores just below the distal junctions. The transverse flagella seldom have a length greater than 0.5 turn around the body and the posterior flagella are usually about equal to the length of a single zooid. These usually do not lie in the sulcus, but are thrown out at a slight angle. The longitudinal flagellum of the posterior zooid may be considerably longer than the other longitudinal flagella.

The nucleus is a spheroidal body, filled with moniliform chromatin strands. It is generally found near the center of the body, slightly to the right of the sulcus. Its transdiameter is about 0.39 transdiameter of the body in length. The number of nuclei usually lags behind the number of zooids in a chain, one being present in a two-zooid chain, two in four zooids, and four in eight zooids, showing a lack of synchronism in the division of nuclei and cytoplasm.

The plasma is translucent, finely granular and generally abundantly filled with nematocysts, food bodies and vacuoles. The nematocysts vary in number and arrangement in different individuals. This species is an omnivorous feeder, appropriating almost any small organism found in the plankton, such as crustacean larvae, copepod eggs, other dinoflagellates, as *Gonyaulax*, *Peridinium*, and *Diplopsalis*, with other organisms indistinguishable owing to their advanced stage of digestion. It is evident from the large size of many of the food bodies thus taken in that two or more individuals of the chain must coöperate in the process of ingestion. The ejection of solid particles has been observed from the sulcus at the region of the posterior pore. This takes place very quickly, the cytoplasm closing up to its normal appearance in about thirty seconds.

The plasma has a rosy tint, varying sometimes to pale green or almost colorless. The depth of the rose color varies greatly in different individuals, and is more pronounced in the peripheral zone of cytoplasm. The surface of the epicone is generally smooth, that of the hypocone striate and furrowed, about ten striae or ribs on 0.5 transdiameter. The surface between the striae may be raised into smoothly rounded ridges.

Activities.—These are very active organisms, their incessant motion making any attempt to determine the coördination or lack of it, in the movements of the different flagella, a matter of great uncertainty. When first placed under the microscope the progression is mainly in loose, anticlockwise spirals with only occasional clockwise rotations, varied with jerking motions of the anterior end upward, and occasionally reversing its spiral direction. Either the ventral or dorsal side may be uppermost when quiescent.

Coördination in the movements under the cover glass of the different sets of flagella is lacking at least part of the time. One or two of the transverse flagella may be in active motion with the others only faintly or not at all motile. When all are moving at the same time the rate of motion is not the same for all nor does motion begin in each at the same time. This is equally true of the longitudinal flagella.

Under the brilliant illumination necessary for microscopic work the organism soon rounds up to a spheroidal form, the girdles becoming completely obliterated and motion ceasing gradually. With cytolysis and dissolution of the body, the nematocysts are usually discharged a few seconds after the breaking down of the body wall.

Dimensions.—Length of individual zooid, 25–45$\mu$; length of 4-zooid chain, 110$\mu$; transdiameter, 70–90$\mu$; diameter of nucleus, 25–30$\mu$; length of nematocysts, 10–20$\mu$.

Occurrence.—This was found abundantly at La Jolla, California, in hauls made from June 27 to July 17, 1906, from near shore to 7 miles offshore and from the surface as well as in hauls from depths up to 595 meters, in surface temperatures varying from 20°4 C to 21°4 C. There is no evidence that it lives in such depths. In July, 1914, and also in July and August, 1915, it was observed in the surface hauls made near shore, though not abundant in either year. In 1917 it was present in the majority of the hauls made between June 26 and August 22, both in the surface hauls made at the end of the pier and at the Biological Station and in the deeper hauls made from 1 to 11 miles offshore from depths up to 80 meters.

Synonymy.—This was figured by Kofoid (1907*b*) as *P. schwartzi.* Chatton (1914*c*) separated it from that species and gave to it specific rank as *P. kofoidi.*

## **Polykrikos schwartzi** Bütschli

Text figure F, 4

Turbellarian larva, Ouljanin (1868), p. 161.

*Polykrikos schwartzi* Bütschli (1873), pp. 673–676, pl. 26, fig. 22; (1885), pp. 964, 965, pl. 55, figs. 8*a-c*.

*Polykrikos swartzii,* Allman (1875), pp. 176, 177, pl. 118, fig. 2.

*Polycricus schwartzii,* Grimm (1878).

*Polykrikos swartzii,* Saville-Kent (1880–82), pp. 83, 858, 860 (*P. schwartzi* and *P. auricularia*).

*P. auricularia* Bergh (1881*a*), p. 9; (1881*b*), pp. 256–259, pl. 16, fig. 72.

*P. auricularia,* Entz (1882), p. 189.

*P. auricularia,* Pouchet (1883), pp. 450–452; (1885*a*), pp. 66, 80; (1885*b*), p. 530; (1887), pp. 108–111, pl. 9, figs. 10–13; (1894), p. 170.

*P. auricularia,* Balbiani (1884), pp. 367–370, fig. 45.

*P. schwartzi,* Bovièr-Lapierre (1886), pp. 535–536; (1888), p. 579.

*P. schwartzi,* Möbius (1888), p. 112.

*P. auricularia,* Schilling (1891*b*), pp. 200, 206.

*P. auricularia,* Lauterborn (1893), p. 210.

*P. auricularia,* Delage and Hèrouard (1896), p. 386, fig. 679.

*P. schwartzi,* Aurivillius (1896), pp. 22, 30; (1898), pp. 204, 282, 288, 296, 390, 392 (as *Polycricus auricularia*).

*P. auricularia,* Jörgensen (1899), tables 18, 72; as *P. schwartzii* (1912), p. 10.

*P. auricularia,* Lemmermann (1899), p. 375; (1902), p. 263.

*P. auricularia,* Pavillard (1905), pp. 49, 80.

*P. auricularia,* Dogiel (1906), p. 37.

*Polycricos auricularia,* Ostenfeld (1906), p. 19; (1909), p. 8; (1913), pp. 123, 141, 339.

*Polykrikos schwartzii,* Paulsen (1907), p. 24; (1908), p. 107, fig. 149.

*P. schwartzi,* Kofoid (1907*b*), in part, pp. 291–293, 1 figure.

*Polycricus auricularia,* Lohmann (1908), pp. 252, 284, 369.

*Polykrikos schwartzi,* Doflein (1911), p. 528, fig. 476.

*P. schwartzi,* Kofoid and Rigden (1912), p. 337.

*P. auricularia,* Cavers (1913), pp. 182, 183, fig. 9.

*P. schwartzi,* Fauré-Fremiet (1913*a*), pp. 366–368; (1913*b*), pp. 289–290, fig. 1.

*P. schwartzi,* Chatton (1914*b*), pp. 434–437, figs. 1–8; (1914*c*), pp. 157–194, figs. 1–13.
*P. schwartzi,* West (1916), pp. 54, 55, fig. 39.
*P. schwartzi,* Lebour (1917*b*), p. 198.

DIAGNOSIS.—Colonial body composed of 2, 4, 8, or 16 zooids, each *Gymnodinium*-like in structure, the length about 0.44 transdiameters, girdle median, without displacement; sulcus extending length of body; surface smooth; nematocysts present; color, green to rosy. Length of chain of eight zooids, 140μ. Baltic, Mediterranean, North Sea, Atlantic, Pacific off La Jolla, California, June-August.

DESCRIPTION.—The individual zooids are small, subcircular in cross-section, with a length of 0.44 transdiameter. The colony of eight zooids has a length of about 4.21 transdiameters at the widest part, with the body having a subcylindrical form with broad apices. The proximal and distal zooids are usually slightly smaller than the other zooids. The lines of separation of the different zooids show the same constriction found in *P. kofoidi.* The epicone and hypocone are subequal. The apex of the proximal zooid is broadly rounded, or may be slightly flattened. The antapex of the distal zooid is also broadly rounded and often notched by the distal end of the sulcus.

The girdle of each zooid is nearly submedian in position. It follows a transverse direction around the body without displacement of its distal end. The furrow has a width of about 0.04 transdiameter and is deeply impressed with the excavation having an anterior extension, undercutting the anterior border and gradually rounding out to the posterior one. Its borders are smooth.

The sulcus extends from near the apex to the antapex of the colony as a continuous furrow. Its width is irregular, becoming wider at each junction with the girdles, narrowing to half that width in the intercingular areas. At the antapex of the distal zooid it forms a broad, shallow notch. The anterior flagellar pores are located at the junction of girdles and sulcus, the posterior pore slightly posterior to those points. The transverse flagella often have a length equal to that of the girdles. The longitudinal flagella have a length slightly greater than the length of the single zooid.

The nucleus is a spheroidal body filled with moniliform chromatin strands. Its transdiameter is about 0.33 transdiameter of the body. As in *P. kofoidi,* the number of nuclei usually equals half the number of zooids of the colony.

The plasma is finely granular, and often contains oil globules and minute refractive granules. The nematocysts vary in number and are not constant in position. Food bodies of varying sizes are common in many of the individuals noted, frequently being huge in size and displacing the contents of the entire body. The color of the cytoplasm varies from a grey green to a rose, though none have been found so deeply colored as those figured by Bergh (1881*b*).

DIMENSIONS.—Length of individual zooid, 15μ; length of chain of 8 zooids, 140μ; transdiameter, 65μ; diameter of nucleus, 20μ; length of nematocysts, 10–20μ.

OCCURRENCE.—This has been found at La Jolla, California, with *P. kofoidi,* though not so abundantly, in hauls made from June 27, 1906, from near shore to 7 miles offshore and from the surface in hauls from various depths up to 595 meters, and in surface temperatures varying from 20°.4 C to 21°.4 C. In 1917 it was found in a few hauls made between June 26 and August 22, both in the surface hauls made at the end of the pier at the Biological Station and in the deeper hauls made from 1 to 11 miles offshore from depths up to 80 meters.

Earlier records of its occurrence are as follows: Ouljanin (1868); Bütschli (1873) off the coast of Norway; Bergh (1881*b*) from the Baltic off the coast of Denmark in July; Pouchet (1883, 1885, 1887) from the Atlantic off Concarneau, France, April to July, and in the Arctic near Iceland in August; Lauterborn (1893) from the North Sea off Helgoland, Germany; Aurivillius (1896) from the Baltic at Kiel, Germany, (1898) from the Skagerack in January and September to November; Jörgensen (1899) off the west coast of Norway at Hjeltefjord in May, at Puddefjord in November and December, and (1912) from the Skagerack in September, November, and December; Pavillard (1905) from the Mediterranean at Etang de Thau near Cette, France, in October and April; Ostenfeld (1906, 1909, 1913) from the North Sea, August, November, the Skagerack and Cattegat in November; Lohmann (1908) from the Baltic at Kiel, Germany, in April, May, and September; and Lebour (1917*b*) at Plymouth Sound, England, from May throughout the summer. It is thus seen to be somewhat cosmopolitan in its habitat.

Comparisons.—This species differs from *P. kofoidi* mainly in the lack of ridges on the surface of the hypocone and in the lack of displacement of the girdle. In *P. kofoidi* the girdle has a displacement of about 0.15 transdiameter. The length of the latter species appears to be somewhat greater than that of *P. schwartzi*.

Synonymy.—This organism was described by Bütschli (1873) as *P. schwartzi*. Bergh (1881*b*) described a second species as *P. auricularia*, which Kofoid (1907*b*) later reduced to a synonym of Bütschli's species, *P. schwartzi*, critical examination of the two forms failing to reveal distinct specific differences. The form figured by Kofoid was separated by Chatton (1914*c*) from *P. schwartzi* and given specific status as *P. kofoidi*.

CHAPTER XVII

# NOCTILUCIDAE: PAVILLARDIA, NOCTILUCA

## Family 4. **NOCTILUCIDAE** Saville-Kent

Noctilucidae Saville-Kent (1880–82).
Noctilucidae, Poche (1913), p. 165.

### Diagnosis

Gymnodinioidae characterized by the presence of a tentacle, more or less mobile, and without ocellus. The tentacle arises in the sulcal area and extends posteriorly. In *Noctiluca* this fundamental relationship is obscured in the large globular form, but is apparent in the small, *Gymnodinium*-like stages. This family contains two genera, *Noctiluca* Suriray and *Pavillardia* gen. nov.

### Historical Discussion

This family was created by Saville-Kent (1880–82) for two genera, *Noctiluca* Suriray and *Leptodiscus* Hertwig. The latter species is known in only one stage of its life history. The *Gymnodinium* or dinoflagellate stage, if such occurs, still remains to be discovered. This fact leaves its generic relations an unsolved problem. Further investigation will be required before it can be more definitely located. We therefore remove it from the family Noctilucidae and place it, with *Craspedotella* Kofoid, in the family Leptodiscidae Kofoid, in the Cystoflagellata Haeckel.

Because of its definite dinoflagellate characters of sulcus and girdle and of the *Gymnodinium*-like stage in its life history *Noctiluca* is closely allied to the Gymnodinioidae. We therefore place it in that tribe, removing it from the Cystoflagellata Haeckel, a group whose genetic relationships as shown in the Leptodiscidae are still obscure.

### Key to Genera of **Noctilucidae**

*Gymnodinium*-like girdle and sulcus persistent, reddish orange pigment present ........................................ **Pavillardia** gen. nov.
*Gymnodinium*-stage temporary, tentacle retained in huge globular stage ........**Noctiluca** Suriray

## PAVILLARDIA gen. nov.

Text figure JJ

Fig. JJ. *Pavillardia tentaculifera* sp. nov. × 500.

Diagnosis.—Gymnodinioidae with *Gymnodinium*-like girdle and sulcus; longitudinal flagellum usually absent; stout, finger-like, mobile tentacle directed posteriorly; no ocellus. Type species *Pavillardia tentaculifera* sp. nov.

### Historical Discussion

The possession of a stout mobile tentacle affords an adequate justification for generic distinction of organisms from those without this characteristic. Indeed, the possession of this organ in *Noctiluca* was one of the prime grounds for the establishment of the order Cystoflagellata. The genus differs from *Protodinifer* in the presence of a complete girdle not posteriorly located, but resembles it strikingly in the shape, location, and behavior of the tentacle. It differs from *Erythropsis* in having a girdle of the slightly displaced *Gyrodinium* type and in the entire absence of the eyespot, although the presence of the brilliant brown pigment in the tentacle is suggestive of the pigmentation in that genus. It differs from *Noctiluca* in the completeness of the girdle and in having the typical form of the Gymnodiniidae instead of that of the inflated, subspherical body of *Noctiluca*.

The genus is named in honor of Professor J. Pavillard, the botanist of Montpellier, whose researches at the Station Biologique at Cette, France, have added much to our critical knowledge of the Dinoflagellata.

## **Pavillardia tentaculifera** sp. nov.

Plate 10, figure 114; text figure JJ

Diagnosis.—A medium sized species with stout ovate body, its length 1.75 transdiameters; girdle slightly premedian, displaced 0.33 transdiameter; sulcus extending from near apex to antapex; surface faintly striate; stout club-shaped tentacle directed posteriorly from antapex; color, pale yellow. Length, 58μ. Pacific off La Jolla, California, July.

Description.—The body is stout ovate, widest posteriorly; circular in cross-section, its length 1.75 transdiameters at the widest part. The hypocone exceeds the epicone in size, its length being greater by 0.16. The epicone is acorn-shaped with minute, acute apical point at the apex. It has a length on the left and right sides of the body of about 0.38 and 0.5 respectively of the total length of the body. The hypocone has a length of about 1.3 transdiameters, expanding midway to about 1.16 transdiameters in width. The antapex is low conical with a club-shaped tentacle extending posteroventrally from its tip.

The girdle is complete, forming a descending left spiral abruptly curved posteriorly at its distal 0.15 to a total displacement of 0.35 transdiameter. The furrow is deeply impressed with slightly protuberant lips, with the anterior shelf undercut and the posterior sigmoid in optical section. Its width for most of its course is about 0.05 transdiameter and in the distal 0.15 this is reduced to a very narrow cleft which, however, completes the circuit. The transverse flagellum does not reach beyond 0.75 of the circuit. It is a fine ribbon thrown into minute undulations traveling distally along its length. The pore for the transverse flagellum lies at the proximal end of the girdle.

The sulcus lies on the flattened ventral face and extends from within a short distance of the apex posteriorly in a straight line to the proximal end of the girdle and thence with a sweeping curve to the left posteriorly to the antapex, ending at the junction with the tentacle. No pore for a longitudinal flagellum was detected. Apparently in lieu of the usual threadlike posterior or longitudinal flagellum this species in common with *Protodinifer tentaculatum* has a stout tentacle-like prolongation on the posterior end of the body and ventral furrow. This tentacle

is club-shaped in *Pavillardia tentaculifera*, 0.75 transdiameter in length and 0.12 in greatest diameter, which is in the middle half of the length. At its proximal end it is constricted to half its middle diameter and contracts distally to a blunt point. Throughout its entire length except at the tip and base it is suffused with a brilliant, burnt orange brown color which is quite uniformly translucent and shows no internal differentiation. It is habitually carried in an oblique position about 30° ventrally from the axis, slightly arched with the concave side ventral.

The surface of the body is covered with a thin pellicle with a narrow clear zone beneath except at the poles where this is obliterated. A few minute yellowish platysomes are scattered somewhat irregularly near the surface and several linear ones mark out (faintly) several striae on the right side of the longitudinal furrow on the epicone.

The cell contents consist of the nucleus located slightly in front of the middle of the body. This is large, 0.66 transdiameter in diameter in dorsal or ventral view and 0.5 in lateral view, due to the cup-shaped depression on the posteroventral face. It is double-contoured, with a heavy membrane and is packed full of extraordinarily thick chromatin threads slightly modulated. Sixteen of these strands, possibly not all distinct, are to be counted on the dorsal face. There is evidence of polarization of the strands. Running posteriorly from the flagellar pore at the proximal end of the girdle is a short canal leading towards a slender conical pusule, probably collapsed, but not clearly connected with the canal. The dorsal surface has a suffused rosy tone from certain radial accumulations of reddish substance located peripherally. A cluster of minute red spheres is lodged near the antapex. There is no trace of a lens or pigment mass such as are found in the eyespot of *Pouchetia*. No distinct chromatophores could be detected, though the body as a whole has a pale yellowish tone. Neither rhabdosomes nor oil drops were noted in the individuals under observation. The brilliant brown tentacle makes the animal a conspicuous object in the microplankton. Luminiscence not tested.

DIMENSIONS.—Length, 58$\mu$; transdiameter at girdle, 27$\mu$, at widest part of hypocone, 31$\mu$; length of tentacle below antapex, 19$\mu$; axis of nucleus, 19$\mu$ and 13$\mu$.

BEHAVIOR.—Cytolysis ensues in ten to fifteen minutes under illumination in the microscope with ordinary daylight, the tentacle persisting entire nearly as long as the nucleus but neither surviving more than a minute after cytolysis sets in. The behavior of the motile organism is much like that of *Protodinifer* described above. The tentacle is somewhat more mobile, being raised frequently to a right angle to the axis or even above this and jerked back with a convulsive jerk. Rotation in the anticlockwise direction is frequent with a gliding anterior movement which must be due to the posteriorly directed current in the ventral furrow. The body is somewhat metabolic. In one individual under observation small protuberances of the body were thrust out on the dorsal and posterodorsal part of the hypocone and quickly retracted, without immediate pathological consequences.

OCCURRENCE.—This was taken July 2, 1917, with a No. 12 silk net, 6 miles off La Jolla, California, in a haul 60 meters to the surface and in a surface temperature of 20°5 C. On July 20 it was again noted in a haul 6 miles offshore from 80 meters to the surface, and on July 25, 11 miles offshore, and on July 27, 4 miles offshore in hauls from 80 meters to the surface and surface temperature of 21°9 C. It was present in hauls made in the previous summer, and was also observed by the senior author in plankton from a red-water outbreak off La Jolla in July, 1907.

COMPARISONS.—*Pavillardia tentaculifera* differs from *Gymnodinium pseudonoctiluca* Pouchet (1892*b*) in being smaller, 58μ instead of 110μ in length, in having a brown instead of a colorless tentacle and in shape and location of the girdle. This is farther anterior and more strongly deflected posteriorly on both ends in Pouchet's species, and in the distal end only in *P. tentaculifera*. Furthermore the epicone is relatively much smaller than the hypocone in his species than it is in the one here described. It shares with this species the tendency of the distal end of the girdle to be strongly deflected posteriorly, and to be reduced nearly to obliteration distally. In this respect they both show earlier stages in a degeneration process (or possibly earlier ones in a development one) which progresses still farther in *Protodinifer* and *Noctiluca*.

The general form of the body, the structure of the girdle and the tendency to striation recall conditions in *Gyrodinium*, especially in species close to *Gymnodinium* in the matter of degree of displacement of the girdle.

It is possible that Pouchet's (1892*b*) *Gymnodinium pseudonoctiluca* should be transferred to this family, though hardly to the genus *Pavillardia*. Its "tentacle" appears to be more like a lateral sulcal pseudopodium and much less like a median tentacle such as those of *Noctiluca* and *Pavillardia*. Pending fuller knowledge of such pseudopodia in *Gymnodinium* it seems wise to leave Pouchet's species in that genus.

## **NOCTILUCA** Suriray

Not "Noctiluca marina" Adler (1852). Not binomial. Annelid.

Not "Noctiluca marina" Linnaeus (1758), p. 654, synonym of *Nereis noctiluca;* nor "Noctiluca marina" Linnaeus (1764), pp. 3, 203, reprint by Adler. Ed. 3 in 1787. Annelid.

"Medusa marina" Slabber (1771, *fide* Ehrenberg, 1834 for date), p. 67, pl. 8, figs. 4, 5; not binomial name. Also edition dated 1778.

*?Nereis noctiluca* Müller, O. F. (1776), p. 217, in part.

*Gleba* Bruguière (1791), pl. 89, figs. 2, 3.

*Medusa scintillans* Macartney (1810), pp. 264–265, pl. 15, figs. 9–12.

*Slabberia* Oken (1815).

*Noctiluca miliaris* Suriray Mss, Lamarck (1816), pp. 470–472.

*Mammaria scintillans*, Ehrenberg (1834), p. 559.

*?Physematium atlanticum*, Meyen (1834), p. 163, *fide* Ehrenberg (1834), p. 522.

*Noctiluca miliaris* Suriray (1836), pp. 1–16, pls. 1–2.

### DIAGNOSIS

The body is inflated subreniform to spheroidal; distinction between epicone and hypocone obliterated, in the adult, by loss of girdle resulting from inflation by hydrostatic vacuoles. Sulcus deeply reëntrant, the medium cytostomal region extended anteriorly in the straight apical trough, girdle represented only by its proximal remnant; longitudinal flagellum short, transverse flagellum reduced to a projecting mobile tooth; tentacle at posterior end of sulcus; cytoplasm vacuolated, anastomosing mobile strands move from periphery to central mass containing nucleus; colorless or bluish green, sometimes tinged with yellow

in central mass. Multiple fission produces zoospores with girdle, one flagellum, and tentacle. Diameter, 200–1200μ. Cosmopolitan in neritic, marine plankton. One species, *Noctiluca scintillans,* the type of the genus.

### Comparisons

This genus differs markedly from *Pavillardia* in the excessive vacuolation of its cytoplasm, in the degeneration of the girdle, reduction of the transverse flagellum, and deep excavation of the sulcus in the region of the cytostome. These contrasts result from the inflation due to the hydrostatic vacuoles.

It resembles *Pavillardia* in the posteriorly located tentacle and in the behavior of this organ, as well as in the extension of the sulcus from near the apex to near the antapex.

### Synonymy

This is discussed in connection with that of the only species, *Noctiluca scintillans* Macartney. The flagellate described from fresh water by Fabre-Domergue (1889), as *Pronoctiluca pelagica,* does not appear to be a dinoflagellate or to have any immediate relation to this genus.

There is but one valid species in the genus, *N. scintillans,* which is here designated as the type. All others described in the genus appear to be synonyms.

## **Noctiluca scintillans** (Macartney)

Text figures KK, 1–6

"Medusa marina" Slabber (1771, *fide* Ehrenberg, 1834, for date), p. 67, pl. 8, figures 4, 5.
*Medusa scintillans* Macartney (1810), pp. 264–265, pl. 15, figs. 9–12.
*Slabberia* Oken (1815).
*Noctiluca miliaris* Suriray Mss, Lamarck (1816), pp. 470–472.
*Mammaria scintillans,* Ehrenberg (1834), p. 559.
"Noctiluca marina," Ehrenberg (1834), p. 559.
*Noctiluca miliaris* Suriray (1836), pp. 1–16, pls. 1, 2.
*N. banksii?* var., Ehrenberg (1834), pp. 509, 510. *Lapsus* for *Noctiluca,* a crustacean.
*N. punctata* Busch (1851), p. 199, fig. 1.
*N. omogenca* Giglioli (1870), p. 490.
*N. pacifica* Giglioli (1870), p. 491.

Diagnosis.—Body inflated, vacuolated, broadly reniform to subspheroidal; girdle reduced to proximal remnant; sulcus forming reëntrant cytostome, extended anteriorly to apex in a straight trough; longitudinal flagellum short, transverse one reduced to a mobile tooth; prehensile tentacle at posterior end of sulcus; nucleus with beaded chromatin, cytoplasm containing nucleus massed near sulcus; scattered phosphorescent oil globules, pellicle firm; no chromatophores; nutrition holozoic. Small zoospores with longitudinal flagellum, girdle and tentacle, formed by multiple fission. Diameter of adult, 200–1200μ, rarely 2000μ. Cosmopolitan in neritic, marine plankton.

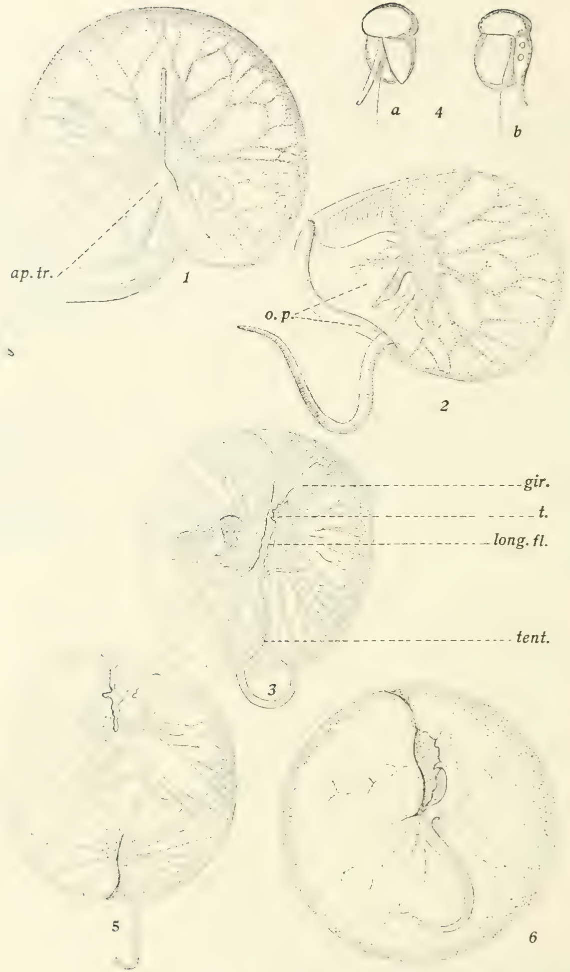


Fig. KK. *Noctiluca scintillans* (Macartney). 1. Dorsal view showing apical trough. After Allman (1872, pl. 18, fig. 1). × 125. 2. Lateral view from the left side showing the deep oral pouch. Modified after Allman (1872, pl. 18, fig. 2). × 125. 3. Posteroventral view showing sulcus, girdle, undulating membrane or tooth, flagellum and tentacle. The anterior lip is at or near the upper margin of the figure. Modified slightly after Robin (1878, pl. 36, fig. 4). × 100. 4*a*, *b*. Zoospores. After Cienkowsky (1873, pl. 6, figs. 38, 42). × 500. 5. *Noctiluca* in chain at mitosis showing girdle in the anterior schizont. After Robin (1878, pl. 41, fig. 24). × 125. 6. Midventral view showing sulcus, rudimentary girdle, transverse flagellum or tooth, longitudinal flagellum and tentacle. Modified after Webb (1855, pl. 6, fig. 7). Magnification not given. Abbreviations: *ant. l.*, anterior lip; *ap. tr.*, apical trough; *g.*, girdle; *l. fl.*, longitudinal flagellum; *o. p.*, oral pouch; *t.*, tooth or transverse flagellum; *tent.*, tentacle.

Description.—The body has various shapes, depending upon the degree of its inflation, age, and food contents. It is especially liable to deformation and wrinkling, due to contraction and local collapse of the periphery on capture and standing in the laboratory. The girdle rarely affects the form materially, and even the sulcus fades out with the rounding up in old individuals and as cytolysis approaches. The dinoflagellate structures, the girdle and sulcus, as well as the effect of these upon the form of the body, are shown more clearly in the smaller individuals. The smaller individuals have a proportionately deeper sulcus and a more reniform contour than the larger ones, which tend to be more spheroidal, with only a slight flattening and shallow excavation along the sulcus. Collapsed, or non-distended, small individuals may have the anterior ends extended and somewhat pointed, or even flattened, by the rather rigid, barlike extension of the precingular trough of the sulcus, and the posterior end may be extended by its postcingular extension, terminating in the tentacle.

In typical, distended, small ($400\mu$) individuals (fig. KK, 1) the body is broadly subreniform, with the transverse diameter slightly exceeding both the dorsoventral and the longitudinal ones. There is, however, much variation in proportions, due to contraction and collapse. The ventral surface is deeply incised by the strictly longitudinal, median sulcus, which terminates posteriorly in the tentacle and runs thence anteriorly in a straight line to its termination in the straight apical trough, at or beyond the morphological apex of the epicone. The depth of the sulcus varies in the several regions and is unlike in different individuals, according to the degree of recession of the cytostome which lies in its deepest midventral region.

There are two main regions of the sulcus, the oral pouch containing the cytostome and the apical trough. The oral pouch, when fully retracted (fig. KK, 2, *o. p.*), is a deep median pocket, laterally compressed, at the bottom of which lies the central protoplasmic mass. The tentacle is placed at its posterior end, the longitudinal flagellum traverses it lengthwise, the tooth lies on its left face, and the proximal end of the girdle creases its left side. In lateral view the floor of the oral pouch runs anteriorly from the base of the tentacle to a level slightly above that of the equator, where it turns abruptly ventrad at right angles, forming the anterior lip (fig. KK, 1, *ant. l.*) at a level with the general contour of the body. The cytostome lies in the bottom of the oral pouch, as a linear region through which food is taken. Its exact limits are unknown.

The apical trough (fig. KK, 1, *ap. tr.*) is the continuation of the sulcus anteriorly towards the apex. It emerges from the oral pouch over the anterior lip as a converging tract, and is continued as a narrow, straight, shallow furrow to its abrupt termination near the apex. It is supported below the pellicle by an accumulation of protoplasmic processes and a thickening of the peripheral protoplasm. The trough may be slightly elevated above the general contour, and appears to be a rather rigid structure. There is no evidence that it can function as a cytostome, as does some part of the sulcus within the oral pouch.

The sulcus in other dinoflagellates with spiral girdle may be divided into precingular, intercingular, and postcingular regions. These regions are recognizable in *Noctiluca*. The precingular one includes the apical trough and that part of the sulcus within the oral pouch which passes over the lip into the pouch and posteriorly to the proximal end of the girdle near the tooth. A part of it within the oral pouch may function as a part of the cytostome. The intercingular region is ill-defined owing to the absence of the distal end of the girdle. There is little if any spiral deflection of the girdle in the zoospore and no evidence of such deflection in the degenerate girdle of the adult. The distance between the proximal end of the girdle (fig. KK, 3, *gir.*) and the origin of the longitudinal flagellum which, in most dinoflagellates, represents approximately the point of union of the distal end of the girdle with the sulcus may be held to represent the intercingular part of the sulcus in *Noctiluca*. The postcingular part extends from the origin of the longitudinal flagellum to the tentacle.

The girdle (fig. KK, 3, *gir.*), present in the zoospores (4) as a constriction below the subhemispherical epicone, completely encircles the body. In the adult the girdle is degenerate.

and, though figured by Webb (1855, pl. 6, fig. 6) and Robin (1878, pl. 36, fig. 4; pl. 41, fig. 24), it otherwise escaped their attention, as it has that of all other investigators of *Noctiluca*. We have found this structure repeatedly in living *Noctiluca* and regard it as the proximal end of the girdle and not a mere wrinkle due to contraction. Its constancy in position, when present, its well marked borders and the supporting peripheral cytoplasm confirm this interpretation. Its location and morphological relations are precisely those of the proximal end of the degenerate girdle. It is a shallow, arched trough, arising on the left side of the sulcus just anterior to the base of the longitudinal flagellum and adjacent to the tooth. It makes from 0.08 to 0.20 turn about the body, dying out distally. It lies near the level of the equator and marks the line of incomplete separation of epicone and hypocone which, in *Noctiluca*, would thus be subequal.

The transverse and longitudinal flagella are represented respectively by the tooth and the small longitudinal flagellum. The former (fig. KK, 3, *tent.*) is a small mobile projection which lies at the left and slightly anterior to the base of the longitudinal flagellum, adjacent to the proximal end of the girdle in the edge of the sulcus. It is a somewhat rigid, striate membrane, overarching the sulcus to its right. Its form varies in published figures and in individuals which we have observed. In its most reduced form it is a small, low, ragged ridge. It may form only a single arched tooth, or a bifid one, or a series of two or three teeth, increasing in length *anteriorly*, or it may rarely appear as a rather ragged tapering or broad and ribbon-like process half as long as the longitudinal flagellum projecting free into the sulcus. In life it is subject to spasmodic downward strokes into the adjacent sulcus and to minute changes in outline. It is not, as we have seen it, freely undulating as is the transverse flagellum typically, but rather rigid and slow in movement. It appears to be a transverse flagellum adapted as a prehensile organ for the capture and ingestion of organisms taken as food. For this function it has become more rigid and has lost its distal extension, locomotor function, much of its mobility, and its location in the girdle. It lies in the sulcus immediately adjacent to the proximal end of the degenerate girdle and runs *longitudinally* instead of transversely. However, it is longest near the end of the girdle. No trace of it is shown in the zoospores by Cienkowsky (1871), Robin (1878), or Ishikawa (1899), provided that the tentacle-like structure shown by Cienkowsky and Ishikawa becomes the tentacle of the adult, as seems probable. No account of the transformation of the zoospores into the adult is available.

The longitudinal flagellum (fig. KK, 3, *long. fl.*) is of the usual form, a simple thread. It is, however, much reduced in length and lies hidden in the oral pouch and is often lost or entirely overlooked. It has little or no function in locomotion.

The tentacle (fig. KK, 3, *tent.*) is the most prominent organ of *Noctiluca*. It arises from the posterior end of the sulcus as a slender process of nearly uniform diameter, from 0.5 to 0.2 the diameter of the body in length. Its diameter is about 0.24 its total length and is slightly increased towards the base. Its distal end is bluntly rounded. It is not cylindrical in cross-section, but flattened, with its dorsal surface convex and the ventral one concave, as though the sulcus were continued upon it. Its dorsoventral diameter is about 0.35 its transverse one. It is transversely striate with close-set, evenly spaced protoplasmic net work, especially in its concave or ventral half, which is its contracted side. It is very fragile, easily broken off, and not infrequently missing in living as well as in preserved material. It is thrown in wide undulations in the vertical plane or in a loose spiral coiled anteriorly. These undulations pass distally, and when the tentacle rests upon an obstacle the body is thrust away from it by the action of the tentacle. The undulations tend in some instances to push objects up into the sulcal region. The base of the tentacle passes over into two laterally spreading fibrillar processes which form a supporting framework for the organ attached to the pellicle.

The cytoplasm is greatly distended by hydrostatic vacuoles in adaption to flotation. It is massed about the nucleus adjacent to the cytostome. This mass sends peripherally to the pellicle slender, branching, and anastomosing strands of protoplasm which unite with a thin network of peripheral cytoplasm. Scattered through the mass of cytoplasm, in the radial strands and

in the periphery, are numerous small oil globules, the centers of the luminescent activity of the animal.

There are no chromatophores. The color is an opalescent greenish blue, sometimes tinged with yellowish green, or even ochraceous yellow in the central mass of cytoplasm.

Nutrition is holozoic. *Noctiluca* is omnivorous, capturing active organisms such as *Peridinium*, *Gonyaulax*, and nauplii, as well as passive diatoms, metazoan ova, and even engulfing inorganic particles such as small grains of sand.

Multiplication by binary fission is frequent. This results in typical dinoflagellate chain arrangement of the two daughter organisms (fig. KK, 4), although the movements of the tentacles and approaching plasmotomy soon obscure this relation. Early binary fission was misinterpreted by Ishikawa (1891) as conjugation. Doflein (1916) states he has seen complete fusion of cytoplasm and nuclei of two individuals. Mitosis (see Ishikawa, 1899; Calkins, 1899; Doflein, 1900; and Jollos, 1910) is of the dinoflagellate type, with large sphere and beaded chromosomes, but the beaded condition is most evident at mitosis.

Multiple fission results in the formation of numerous zoospores (fig. KK, 3) with girdle, longitudinal flagellum, incipient tentacle, and the general appearance of a small dinoflagellate, but with no transverse flagellum.

DIMENSIONS.—Diameter, 400–1200µ, rarely 200–2000µ; zoospores, length, 25–30µ; transdiameter, 10–15µ.

OCCURRENCE.—Abundant in San Diego Bay, San Pedro harbor, San Francisco Bay, and Puget Sound, and less so in the plankton off the Pacific Coast of the United States, throughout the year, but more abundant in summer and autumn. It is apparently cosmopolitan in the neritic plankton of temperate and tropical seas, but not typically pelagic in the high seas. It is not mentioned in Hensen's (1911) summary of the findings of the Plankton Expedition. Karsten (1905*a*, *b*, 1907) lists it in the Valdivia collections only from coastal regions. Parker and Haswell's (1897) statement that *Noctiluca* is the cause of the diffused phosphorescence of the sea should be modified by the restriction to *one* of the causes of phosphorescence in *neritic* waters. "*Pyrocystis*" replaces it in the plankton of the high seas.

SYNONYMY.—The nomenclature of *Noctiluca* is fraught with difficulties arising from fragmentary and incomplete descriptions by the earlier observers, confusion, on their part, of *Noctiluca* with other phosphorescent organisms, as well as by its description under various names. The name *Noctiluca miliaris* has, except for the deliberate reallocation of the organism by Ehrenberg (1834), held almost undisturbed sway in practically all the voluminous, original literature and in widespread citation in standard texts since 1816, when Lamarck used Suriray's manuscript name in his *Animaux sans vertebres*. The law of priority clearly calls for the specific name *scintillans* Macartney (1810), but the determination of the generic name is fraught with difficulties. Any name other than *Noctiluca* rests on the most unstable premises, and even it is of questionable validity.

The most extended discussion of the status of *Noctiluca* is found in the exhaustive review by Ehrenberg (1834) in his *Das Leuchten des Meeres*, though it is not made with a view to priority under any code of nomenclature. From

this review and a survey of all available literature it appears that *Noctiluca* may be found in the older literature under the following generic names: *Nereis* (?), *Medusa*, *Mammaria*, *Gleba*, *Slabberia*, and *Physematium*, prior to Lamarck's publication of Suriray's *Noctiluca* in 1816. All figures and descriptions prior to Slabber's (1771, *fide* Ehrenberg, 1834, for date) account of his "*Medusa marina*" (his plate 8) are so imperfect as not to be recognizable with certainty as *Noctiluca*. Slabber's nomenclature is clearly not intentionally binomial. His figure is recognizable as *Noctiluca*. Oken (1815) gave it the generic name *Slabberia*, but with the rejection of *Slabberia* as doubtfully tenable *Noctiluca* comes next as claimant for priority, and may be accepted even though some extremist might hold that Linnaeus's use of *Noctiluca marina* in Ed. 10 (1758) of his *Systema Naturae* as a synonym in binomial form of his *Nereis noctiluca* (annelid), establishes *Noctiluca* as a genus. Publication of the name in the later edition (1787–1790) of his *Amoenitates Academicae*, in which he republishes Adler's (1752) paper on "*Noctiluca marina*" in which these words are used as a title and not as a binomial name of the annelid worm described in the paper, might also be used in support of the preoccupation of *Noctiluca* Suriray by Adler's name. We reject this interpretation since Adler's use of the words in binomial form was not an intentional binomial naming of the worm.

The first valid specific name appears to be Macartney's *Medusa scintillans*, published in the well known *Transactions of the Royal Society of London* (1810). Its priority was recognized by Ehrenberg (1834) and later by Mobius (1861). The date of Macartney's paper is incorrectly stated in Carus and Engelmann's *Bibliotheca Zoologica* (1861, vol. 1, p. 294) as 1820. Macartney's account and figures are sufficiently complete to afford a recognition of the organism. The tentacle is suggested, though not clearly described, and is figured faintly (his pl. 2, fig. 12).

Later Ehrenberg (1834) decided, on grounds not clearly stated, that the name should be *Mammaria scintillans*. The genus *Mammaria*, founded by O. F. Müller in 1776 for imperfectly described coelenterates, is so inadequately known as to be unrecognizable. It is evident that Müller's (1776) citation of "N. act. N. Curios, vol. 4" is incorrect. No previous publication of *Mammaria* can be located in the memoirs cited by him. The allocation of *Noctiluca* therein is without any satisfactory basis of discussion or revision of the genus by Ehrenberg. We reject his allocation as untenable.

In the course of his discussion Ehrenberg sometimes (1834, p. 559) loosely used the phrase "*Noctiluca marina*" in italicized binomial form simulating a generic-specific combination of names, without, apparently, intending to give it binomial status.

*Noctiluca banksii* var. of Baird (1830, fig. 100*a*) is a crustacean *Noctiluca* and was cited by Ehrenberg (1834, p. 510) as *Noctiluca banksii?* var.

Busch (1851) based his species of *N. punctata* upon the punctate appearance which he observed, but this is not a species character.

Giglioli (1870) describes two new species of *Noctiluca, N. omogenea* and *N. pacifica,* but neither appear to be distinct from *N. scintillans.*

There appears thus to be but a single species, *Noctiluca scintillans* (Macartney), in this genus. It is evident that this name is the only one defensible under the code of nomenclature. It is the type of the genus *Noctiluca.*

Comparisons.—It is obvious that the adaptation of *Noctiluca* to passive flotation by hydrostatic vacuoles has brought about profound modification of structure. The locomotor organs, the two flagella, are no longer functional as a rotater and propellor respectively. The longitudinal flagellum is hidden in the reëntrant atrium and the transverse one is reduced to a mere prehensile tooth. With the degeneration of the latter the girdle disappears, except for its proximal region, and the separation between epicone and hypocone is lost. The sulcus is developed as a large cytostome and the form of the body, as a result of inflation by the vacuoles, loses all marked dinoflagellate characteristics, except as indicated by the sulcus.

The tentacle in its location, structure, and function is foreshadowed or paralleled by the pseudopodium-like tentacle of *Gymnodinium pseudonoctiluca,* the tentacle of *Pavillardia,* the incipient prod of *Proterythropsis,* and the fully developed one of *Erythropsis.* This tentacle of *Noctiluca* can not be the homologue of these structures and at the same time represent the transverse flagellum, as Bütschli (1885) proposed, since the transverse flagellum is present in other tentaculate dinoflagellates and is fully functional. It is rather, as Kofoid (1919) has shown, not a homologue of either flagellum, but a derivative of the margin of the sulcus as are the other tentacles of the dinoflagellates. There is no satisfactory evidence that the tentaculate dinoflagellates form a coherent family, but rather that they are of independent origin in several families. It is still probable, however, that the tentacles are to be regarded as homologous organs throughout the series.

CHAPTER XVIII

# POUCHETIIDAE: PROTOPSIS, NEMATODINIUM

## Family 5. **POUCHETIIDAE** fam. nov.

Diagnosis.—Gymnodinioidae with ocellus located on left side of the intercingular sulcus, consisting of a lens and melanosome or pigment mass; epicone and hypocone are subequal; girdle and sulcus with more or less torsion; pusules usually present; plasma usually colored. Length, 32–141μ. All eupelagic and marine and are known principally from warm temperate and tropical seas and rarely in purely neritic waters.

### Description

The ocellus is located on the left side of the intercingular sulcus, and consists of a lens and melanosome or pigment mass, the latter often amoeboid, and usually differentiated in the center into a red, brown, or yellow region or sensory core. The pigment mass is red throughout in some instances. The epicone and hypocone tend to be subequal except in *Erythropsis*, where the epicone is reduced. The girdle and sulcus in some cases show considerable torsion, and the latter often has an apical and an antapical loop. Paracingular lines are present in *Erythropsis*. Varying degrees of integration of the ocellus occur throughout the genera of this family. Nematocysts are present in *Nematodinium*. A posteriorly directed prod or tentacle is formed in *Proterythropsis* and *Erythropsis*. Pusules are often present, opening anteriorly into the anterior and posteriorly into the posterior flagellar pores. The nucleus generally lies anterior to the ocellus and may or may not have a perinuclear membrane. Longitudinal striae on the surface of the body are rarely present. Vacuoles tend to form in the peripheral plasma.

The plasma is often highly colored, especially peripherally. Cyst formation is very frequent, the closely adherent membrane becoming distended after its formation by an intramembranous fluid. The body itself within the cyst does not become inflated with intracytoplasmic vacuoles.

It contains five genera: *Protopsis* with 3 species, *Nematodinium* with 3, *Pouchetia* with 20, *Proterythropsis* with 1, and *Erythropsis* with 10, making a total of 37 species. Of these five genera three are new, *Protopsis*, *Nematodinium*, and *Proterythropsis*. *Erythropsis* was described by Hertwig (1884), though its affinities with the Dinoflagellata long remained unrecognized, and Pouchetia was proposed by Schütt (1895) for the ocellate Gymnodinioidae, including two species now referred to *Erythropsis*, whose affinities he did not recognize.

### Key to the Genera of the **Pouchetiidae**

1. *Gymnodinium*- or *Gyrodinium*-like, girdle without displacement, sulcus without torsion ........ **Protopsis** gen. nov.
1. Girdle displaced in a descending left spiral, sulcus with some torsion ........ 2
2. With nematocysts ........ **Nematodinium** gen. nov.
2. Without nematocysts ........ 3
3. Without posteroventral prod or tentacle ........ **Pouchetia** Schütt
3. With prod ........ 4
4. Epicone and hypocone subequal, no paracingular lines ........ **Proterythropsis** gen. nov.
4. Epicone less than hypocone, paracingular lines present ........ **Erythropsis** Hertwig

## **PROTOPSIS** gen. nov.

Text figure LL

Diagnosis.—Pouchetiidae with the girdle and sulcus of the *Gymnodinium* or *Gyrodinium* type with simple or compound ocellus, no tentacle, no apical loop of the sulcus, and no torsion of the body. Girdle does not make more than one turn around the body. No paracingular lines. Posterior flagellar pore not located far posteriorly. Three species, all eupelagic and marine. Type, *Protopsis nigra* (Pouchet).

### Description

To include as Lemmermann (1899) has done in the one genus *Pouchetia* all Gymnodinioidae with an ocellus but no tentacle is fraught with extreme difficulty when an attempt is made to define this inclusive genus. Since the course and differentiation of the girdle and sulcus is so largely utilized in generic distinctions, it seems both logical and consistent to apply these criteria within the ocellate forms. This necessitates the separation of those species without torsion of the sulcus or its extension in an anterior loop, and with far posterior location of the posterior flagellar pore, from those having these striking modifications in structure.

The group of simpler Pouchetiidae thus detached from the more complex ones contains but two species, both previously described and imperfectly known, that of Pouchet's (1887, pl. 10, figs. 2 A, B, 3, 4) *Gymnodinium polyphemus* var. *nigrum*, and that of Wright (1907, pl. 1, fig. 8) *Pouchetia ochrea*. The former is the type species of the genus *Protopsis*. To these a third new species, *P. neapolitana*, is added.

It is significant of the possible mode of evolution of the more complex Pouchetiidae that *Protopsis nigra* has a compound ocellus with several lenses and lobed melanosome, while *P. ochrea* has at least a lobed melanosome and *P. neapolitana* a finely divided one.

This fact taken in conjunction with the simplicity and primitive stage of differentiation of sulcus and girdle in *Protopsis* suggests that the divided condition of the ocellus and melanosomes may be the more primitive one since it is

found in association with the primitive or *Gymnodinium*- or *Gyrodinium*-like condition of such fundamental structures as the ordinal characters, the sulcus and the girdle. This genus differs from *Pouchetia* in the absence of apical loop of the sulcus, lack of torsion, and short intercingular region of the sulcus. It differs from *Erythropsis* in the lack of apical loop, paradinial lines, tentacular recess and tentacle. It is plainly the least specialized genus of the Pouchetiidae. It is noteworthy that within this genus, as also in *Pouchetia* and *Erythropsis*, there are two lines of differentiation, namely, into the compound and simple types of ocellus. Speciation has followed parallel courses in the three genera.

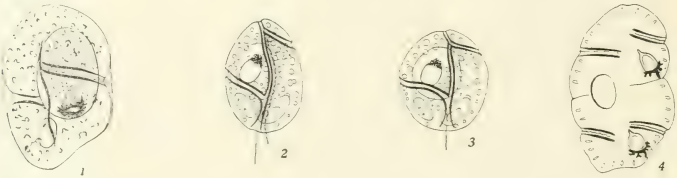


Fig. LL. *Protopsis* gen. nov. 1. *P. nigra* (Pouchet). After Pouchet (1887, pl. 10, fig. 2 A). 2. *P. neapolitana* Kofoid. 3. Same rounding up. 4. *P, ochrea* (Wright). After Wright (1907, pl. 1, fig. 8). × 500.

### Key to the Species of **Protopsis** gen. nov.

1. Ocellus diffuse .................................................. 2
1. Ocellus concentrated, with single campanulate lens, no scattered peripheral pigment .................................................. **ochrea** (Wright)
2. Ocellus with 4–6 spheroidal lenses, ragged melanosome and scattered pigment in peripheral plasma .................................................. **nigra** (Pouchet)
2. Ocellus with single lens, melanosome composed of a cluster of granules .................................................. **neapolitana** sp. nov.

## **Protopsis neapolitana** Kofoid MSS.

Plate 9, figure 96; text figures LL, 2, 3

Diagnosis.—Small species, body ovoidal, its length 1.45 transdiameters; apex pointed; girdle a steep descending left spiral, displaced 0.68 total length; ocellus centrally located, lens subovoidal, flattened against small melanosome composed of clustered granules and 0.5 diameter of lens; plasma almost colorless; holozoic. Length, about 50$\mu$. Mediterranean at Naples, January.

Description.—The body is ovoidal, slightly wider posteriorly, its length 1.45 transdiameters at the widest point which is postequatorial. The epicone is exceeded by the hypocone by 0.25 length of the hypocone. Its length at the proximal and distal ends of the girdle is 0.09 and 0.67 total length respectively. The apex is rotund subconical, about 80° distally, rounding almost to subhemispherical under the stimulus of strong light. The hypocone has a length of 0.91 and 0.33 total length at its anterior and posterior ends of the girdle respectively and the antapex is almost hemispherical with no sulcal notch.

The girdle forms a steep, uniform, descending left spiral of about 30° from the horizontal. It passes from its anterior junction with the sulcus 0.09 total length from the apex to its distal junction 0.67 total length with little change in obliquity. Its total displacement is 0.58 total length or nearly 1 transdiameter. The furrow is about 0.08 transdiameter in width and is lightly impressed without prominent lips. The sulcus runs from near the apex almost to the antapex, with only a slight sigmoid curve. The anterior flagellar pore is at the anterior junction of girdle and sulcus and the posterior a girdle's width below the posterior junction. The transverse flagellum is less than 0.5 the length of the girdle and the posterior one 1.25 lengths of the body in length.

The ocellus is 0.28 transdiameter in length and at the right of the center of the body. It is diffusely organized. The lens is a broadly ovoidal, translucent body 0.22 transdiameter in length and 0.9 of its length in width, and truncated at the end applied to the melanosome. There are no laminae visible. The melanosome consists of a dense cluster of coarse black or very dark brownish black granules clustered in a small hemisphere 0.5 diameter of the lens in diameter applied to the center of the truncated anterior end of the lens.

The nucleus is a small ellipsoidal body lying obliquely in the posterodextral part of the body. Its major and minor axes are 0.40 and 0.26 transdiameter in length respectively. It is filled with coarse, beaded, chromatin strands running spirally about the major axis. No pusules were noted. The body was crowded with food and the products of metabolism. Near the center was a very large, ellipsoidal, fluid-filled vacuole of a very pale, ochraceous-salmon color. Crowded about it were numerous highly refractive bluish green spherules of varying sizes; while crowded into the posterosinistral corner was an ellipsoidal food ball of yellow ochre color with a brownish mass within it. Faint traces of longitudinal striae could be detected on the surface.

Dimensions.—Length, about $50\mu$; transdiameter, $34\mu$.

Occurrence.—One individual observed in the plankton of the Bay of Naples on January 27, 1908, by the senior author.

Activities.—The animal circled in close clockwise spirals several lengths of the body in diameter. The transverse flagellum was seen to be thrown out of the girdle and trailing behind the body, near the longitudinal one, as a spiral band at times while the animal was moving. As cytolysis approached the distal end of the longitudinal flagellum formed an amoeboid mass of plasma which retreated towards its base. This organism was photosensitive to the illumination of the microscope, contracting into a more rounded-up form when intensely illuminated and extending again into the pointed form of apex in dimmer light.

Comparisons.—This species has the *Gyrodinium* type of girdle and sulcus while *P. nigra* (fig. LL, 1) has the *Gymnodinium* type and *P. ochrea* (fig. LL, 4) stands about midway between the two in this feature. This species is placed in *Protopsis* rather than *Pouchetia* because of the absence of torsion in the sulcus. The ocellus also shows an advance in that the lens is a unit instead of several as in *P. nigra*. It is, however, less hyaline than usual in such structures. The melanosome is unique in being composed of a loose aggregate of uniform, small, dark brownish black grains grouped in a small hemisphere on the truncate end of the lens. It is relatively unusually small, having only 0.5 the diameter of the lens and less than 0.1 its volume. The lack of integration in this organ is also seen in the fact that it does not, at least in the single individual observed, have the customary position near the periphery at the left of the

intercingular sulcus, but lies to the right and deep in the center of the body. Its lens is also directed posteriorly. Its functional efficiency as an organ of light perception can at the best be but slight.

### **Protopsis nigra** (Pouchet)

Text figure LL, 1

*Gymnodinium polyphemus* var. *nigrum* Pouchet (1887), pp. 93, 97–104, 112, pl. 10, figs. 2 A, B, 3, 4. Figures 2 C and 5 are not *Protopsis nigra*, but indeterminate. Figures inverted.

*G. polyphemus* var. *nigrum*, Schütt (1895), p. 95.

*Pouchetia nigra*, Lemmermann (1899), p. 360.

*P. nigra*, Pavillard (1905), in part, pp. 47–48. *P. juno* tentatively included.

*Gymnodinium polyphemus* var. *magna* Dogiel (1906), p. 37. *Lapsus* for *nigrum*.

Diagnosis.—A medium sized species, body asymmterical ovoidal, its length 1.5 transdiameters; girdle equatorial, displaced 0.3 transdiameter; sulcus straight, midventral; ocellus dispersed, with 5–8 spherical lenses, amoeboid black melanosome and red core; plasma ochraceous with scattered black granules in periphery. Length, 74μ. Coasts of France, spring and autumn.

Description.—The body is asymmetrically ovoidal, its length 1.5 transdiameters; epicone and hypocone subequal. Epicone subhemispherical, apex broadly rounded, nearly symmetrical, less rotund at the right. Hypocone a trifle smaller than the epicone, much less hemispherical, prolonged at the right side, and with rounded antapex displaced to the left.

Girdle equatorial, forming a descending left spiral displaced about 0.3 transdiameter and not overlapping in the intercingular area. The furrow is deeply impressed with prominent lips and is about 0.12 transdiameter in width. The sulcus does not appear to be fully delineated. As shown, however, it appears to be nearly straight, midventral, and not extended far upon the epicone. It flares distally.

The ocellus is dispersed or compound, consisting of five to eight spherical lenses of varying sizes and grouping and an amoeboid pigment mass with black, lobed melanosome and small, brilliant red, centrally located core. It is located opposite the intercingular region of the sulcus and does not appear to be protuberant or so close to the sulcus as in any way to modify it. The peripheral plasma is crowded with black pigment in the form of small granules and coiled rods in the form of commas, hooks, and irregular semicircles, somewhat more finely divided on the right side of the epicone and less abundant near the melanosome, thus exhibiting a polarization in the direction of the plane of fission. The nucleus is ellipsoidal with its major and minor axis 0.6–0.8 and 0.37–0.66 transdiameter in length respectively. It exhibits the typical parallel chromatic threads. The general color is dark olive ochre, but distinct chromatophores are not indicated. Pouchet (1887) notes the resemblance of its color to diatomin. Often encysted in a closely fitting, transparent cyst.

Dimensions.—Length, 74μ; transdiameter, 45μ; length of ocellus, 15μ; diameters of nucleus, 40μ and 28μ.

Occurrence.—Abundant at Concarneau, France, in the marine plankton, April 28 and May 2 and 3. Pavillard (1905) reports it (*sensu latu*) as rare in the plankton of the Etang de Thau, at Cette, France, on the Mediterranean in October and December. The surface temperatures range there from 18°4 C to 6°9 C in these months.

COMPARISONS.—The ocellus and dimensions separate this from *P. ochrea* (fig. LL, 4). Its ocellus is of the same general form as that in *Nematodinium partitum* (fig. NN, 4), *Pouchetia schuetti* (fig. PP, 10), and *Erythropsis labrum* (fig. SS, 6), indicating parallel lines of evolution of the ocellus in the four genera, *Protopsis, Nematodinium, Pouchetia,* and *Erythropsis.*

SYNONYMY.—This species was originally described by Pouchet (1887) as *Gymnodinium polyphemus* var. *nigrum* and represented one of two varieties into which he divided his *G. polyphemus* (1885*b*, pl. 26, figs. III, IV). Neither variety, however, represents his original form in those characteristics which, with fuller knowledge of these organisms, are now recognized as diagnostic, and all three appear to be distinct species. The imperfections of Pouchet's figures and descriptions and his probable inclusion of more than one form under one name, as, for example, in his *G. polyphemus* (1885*b*), add to the difficulties in subsequent specific identifications of these forms. The results are that later workers in this field, Schütt (1895), Pavillard (1905), and Paulsen (1908), have added to the confusion and to the difficulties in synonymy.

Pouchet's *G. polyphemus* var. *nigrum,* as originally figured (1887, pl. 10, figs. 2–5), is distinctly ochraceous and possibly has chromatophores, though none are figured as distinct structures. In so far as indicated the sulcus is longitudinal, midventral, and without torsion. The peripheral cytoplasm contains everywhere finely divided black chromatin in the form of commas and semicircles of irregular shape. These, however, are lacking in his figures 2 C and 5 of an encysted form, in which also the eyespot is of a wholly different type. It is here simple with stout clavate lens and hemispherical melanosome, whereas in the other figures the ocellus is compound with five to eight spherical lenses and an amoeboid pigment mass. In view of the fact that the structure of the ocellus is diagnostic in the group as a whole, and in our experience is not subject to changes within the individual and species so great as here indicated by Pouchet, we conclude that he has included in this species another without peripheral pigment and with simple ocellus. Since its sulcus and girdle are in no way indicated their allocation is impossible. We therefore exclude from *Protopsis nigra* (Pouchet) his figures 2 C and 5 as indeterminate Pouchetiidae.

Lemmermann (1899) allocates Pouchet's *Gymnodinium polyphemus* var. *nigrum* to *Pouchetia* and advances it to specific status, both of which changes Schütt (1895), the authority for the genus, omitted to make, probably because of the fact that he made no revision of forms belonging to *Pouchetia,* rather than by reason of the structural peculiarities of *P. nigra.*

Pavillard's (1905) tentative inclusion of Schütt's *Pouchetia juno* in the synonymy of *P. nigra* appears to us wholly unwarranted by differences in sulcus, girdle, ocellus, coloration, and dimensions.

Paulsen (1908) makes the suggestion that Schütt's *Pouchetia rosea* (Pouchet), which is not Pouchet's species, may be *P. nigra* (Pouchet) Lemm. As we indicate in our discussion of Schütt's species which we regard as

*P. schuetti* nom. sp. nov., Schütt's (1895) forms differ from Pouchet's (1887) in having the torsion of *Pouchetia* and a rosy instead of an ochraceous plasma. The ocellus of *P. schuetti* is compound as in *Protopsis nigra,* but none of Schütt's figures of his "*P. rosea*" has peripheral black pigment. As matters stand Pouchet's (1887) figures must be assumed to be correctly drawn until some one rediscovers his species and critically reëxamines it in the light of later data and these criticisms.

## **Protopsis ochrea** (Wright)

Text figure LL, 4

*Pouchetia ochrea* Wright (1907), p. 4, pl. 1, fig. 8.

Diagnosis.—A small species of rotund body, its length 1.2 transdiameters; girdle equatorial, displaced about 0.25 transdiameter; sulcus?; ocellus simple, lens conical campanulate with terminal projection, melanosome lobed; chromatophores linear, ochraceous. Length, 55μ. Canso, Nova Scotia, July.

Description.—Only one individual in binary fission prior to mitosis is figured by Wright (1907), so that the possibility of an adequate comparative description is much restricted. The body is rotund, its length about 1.2 transdiameters, with epicone and hypocone subequal. Epicone subhemispherical, hypocone less hemispherical with antapex slightly longer at the right, but broadly rounded.

Girdle nearly equatorial, not overlapping, without torsion of the body, intercingular displacement about 0.25 transdiameter, furrow shallow with prominent lips. Sulcus not figured, but probably nearly straight and midventral.

Ocellus simple, located at the left of the intercingular sulcus with its main axis oblique, deflected about 40° from the median plane to the right anteriorly, its length 0.4 transdiameter. Lens simple with campanulate base bearing a short, terminal, anteriorly directed stem about half the length of the base, the bottom of which is buried in the shallow melanosome which bears on its posterior face five or six simple or branched lobes or processes. Chromatophores ochraceous, in strands as in Schütt's *Gymnodinium geminatum.* Nucleus (food ball?) ellipsoidal, its length about 0.33 transdiameter. Binary fission in close fitting gelatinous cyst.

Dimensions.—Length, 55μ; transdiameter, 45μ; length of ocellus, 22μ.

Occurrence.—Common in the plankton at Canso, Nova Scotia, in July, 1901–02 (Wright, 1907).

Comparisons.—Differs from all known Pouchetiidae in having chromatophores and therefore in being in all probability holophytic. The type of ocellus distinguishes it at once from the other species of this genus, *P. nigra* (Pouchet). However, the peculiar form of the lens and the much lobed melanosome are indicative of a near approach to or only a slight differentiation from the compound type. This species also lacks the distributed peripheral pigment strands so characteristic of *P. nigra* (fig. LL, 1).

## **NEMATODINIUM** gen. nov.

Text figures MM, NN

### Diagnosis

Pouchetiidae with nematocysts; girdle with more than 1 turn, displaced more than 0.5 transdiameter; sulcus with torsion of 0.75 turn or more with a posterior turn on the dorsal side of the antapex; no paracingular lines; ocellus distributed or concentrated, located far posteriorly; eupelagic, marine, holozoic. Type species *Nematodinium partitum* sp. nov.

As yet only three species are known in this genus, i.e., *N. armatum* (= *Pouchetia armata* Dogiel, 1906), from the marine plankton off Naples, Plymouth, and La Jolla, and *N. torpedo* and the type, *N. partitum,* from off La Jolla. This small number of species renders further generic characterization superfluous.

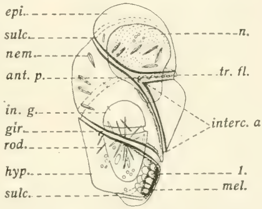


Fig. MM. *Nematodinium partitum* sp. nov. Abbreviations: *ant. p.*, antapical pore; *epi.*, epicone; *gir.*, girdle; *hyp.*, hypocone; *in. g.*, ingested *Gymnodinium* sp.; *interc. a.*, intercingular area; *l.*, lens; *mel.*, melanosome; *n.*, nucleus; *nem.*, nematocyst; *rod.*, rodlets; *sulc.*, sulcus; *tr. fl.*, transverse flagellum. × 500.

### Comparisons

The diagnostic characteristic of this genus is the possession of nematocysts clustered about the nucleus. These are known elsewhere in the Dinoflagellata only in *Polykrikos.* These nematocysts are small, sometimes slightly capitate, tapering, peg-shaped bodies, 5µ to 22µ in length, filled with fluid with an introvert consisting of a cone contracting to a straight axial tube extending nearly to the opposite end of the body, where it turns abruptly and coils about the axial shaft in a close flat spiral. On discharge the tube is presumably everted as a long coiled thread. The presence of these complex structures affords a sufficient basis for generic distinction. There is no evidence that these organs are introduced from extraneous sources.

Associated with the presence of these organs is the extreme posterior location of the ocellus close to the posterior end at the left of the lower part of the sulcus. The ocellus is transversely oriented (fig. MM, *l.*). Of three species known, all have at least 1.5 turns of the girdle and the sulcus exhibits an unusual degree of torsion. In *N. partitum* there are at least 1.5 turns of this structure, of which only about 0.5 is intercingular, the remainder constituting the anterior and posterior loops, while in *N. torpedo* there are two turns. This anterior loop may be present in other highly specialized Pouchetiidae as in *Pouchetia violaceum* and in several species of *Erythropsis.* Specialization in their fundamental structures such as the girdle and sulcus is thus accompanied by specialization elsewhere in the organism, as in the nematocysts of *Nematodinium* and tentacle of *Erythropsis,* not to mention the ocellus of these genera and of *Pouchetia.*

We find in *Nematodinium* the same types of ocellus which have appeared in other genera of the Pouchetiidae, in *Protopsis*, *Pouchetia*, and *Erythropsis*. These two types have been utilized by us to distinguish subgenera in the last two genera. However, in view of the small number of species as yet known in *Nematodinium*, no subgenera are here established therein, although the same basis exists therefor.

### KEY TO SPECIES OF **Nematodinium**

1. Ocellus distributed, numerous small spheroidal lenses, melanosome diffuse .................... **partitum** sp. nov.
1. Ocellus concentrated .................... 2
2. Lens spherical, melanosome subhemispherical .................... **armatum** (Dogiel)
2. Lens elongated, melanosome very small, band-shaped .................... **torpedo** sp. nov.

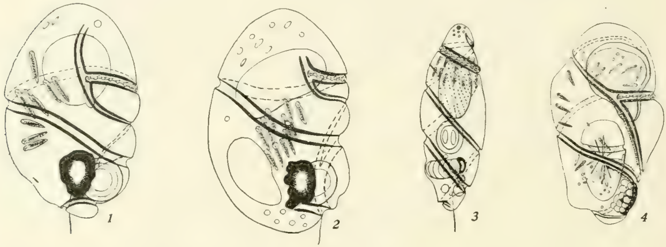


Fig. NN. *Nematodinium* gen. nov. 1. *N. armatum* Dogiel). 2. Second individual of the same species. 3. *N. torpedo* sp. nov. 4. *N. partitum* sp. nov. × 500.

### **Nematodinium armatum** Dogiel

Plate 11, figure 122; text figure NN, 1, 2

*Pouchetia armata* Dogiel (1906), pp. 36–38, 42, pl. 2, figs. 48, 49. Symmetry reversed in drawing.
*P. armata,* Klebs (1912), p. 430.
*P. armata,* Cavers (1913), p. 183.
*P. armata,* Lebour (1917*b*), p. 198.
*P. armata,* Chatton (1914), p. 435.

DIAGNOSIS.—A medium sized species, body subellipsoidal, its length 1.55 transdiameters; girdle a descending left spiral of 1.5 turns, displaced 0.75 transdiameter; sulcus extending far on epicone and coiled distally around hypocone with a total of 1.25 turns; ocellus far posterior, simple, lens spheroidal, pigment mass subhemispherical, black; nematocysts grouped about the nucleus. Length, 95-100μ. Mediterranean; Plymouth Sound; Pacific at La Jolla, July, August.

Description.—The body is asymmetrically subellipsoidal, flattened on the twisted ventral face between pores, more convex dorsally, tapering somewhat posteriorly. The epicone is larger than the hypocone, with the apex broadly rounded and antapex button-shaped, encircled dorsally by the distal end of the sulcus. The anterior and posterior flagellar pores are located on opposite faces due to the torsion of the body.

The girdle forms a descending left spiral of 1.5 turns. Its proximal end is 0.35 of the total length of the body from the anterior end and its distal end 0.16 from the posterior end. Its total displacement measured in the anteroposterior direction is 0.75–0.85 transdiameter or about 0.5 of the total length. The furrow is deeply impressed with prominent lips. The sulcus extends from near the apex spirally in descending left spiral of 1.25 turns of a narrow groove. There is only 0.5 turn in the intercingular region, the remaining 0.75 being mainly in a posterior curve around the "dorsal" side beyond the emergence of the posterior flagellum. It is possible that the dorsal part of this posterior region is not true sulcus. The posterior part of the sulcus lies in a deep ventral depression at the right side of the ocellus. It is also possible that there is more of an anterior loop than appears in the figures. The anterior and posterior flagellar pores are at the anterior and posterior junctions of sulcus and girdle respectively. The transverse flagellum traverses the whole length of the girdle.

The ocellus is located far posterior, on the left side of the distal end of the sulcus, but still mainly within the intercingular region of that groove. This location appears more clearly in the text figure than in the other figures (pl. 11, fig. 122, and text fig. NN, 2) from a slightly different angle, owing largely to the deep ventral depression in which this part of the sulcus lies. The ocellus has a length of 0.5 transdiameter and its main axis is almost horizontal and is directed ventrally. It is of the simple type with a spherical lens of several concentric laminae of equal thickness of a pale lemon-yellow color. One face is slightly covered by the irregularly hemispherical black pigment mass, half again as large as the lens. A lighter core without noticeable color lies in its center.

The most noteworthy feature of this animal is its nematocysts. These lie in a group of eight to eleven clustered near the nucleus and are all directed more or less anterodorsally. They are greenish peg-shaped bodies, faintly capitate, from 14–22$\mu$ in length and 3–4$\mu$ in greatest diameter. Each shows within a faint coil, the introverted thread. The arrangement varies somewhat in different individuals, but the general direction and location are similar in all. The differences in size are similar to those found in *Polykrikos,* and seem to be correlated with varying degrees of distinctness of the thread. This is an indication of stages in development or age of these organs. There is no evidence in our material that they are derived from or associated with any organism used as food, and they are not located in vacuoles.

The nucleus is spheroidal, about 1.5 transdiameters in diameter and is located in the anterior half of the body. As binary fission approaches it becomes obliquely elongated or reniform, and lies with its long axis about 70° from the major axis. It is filled with fine, parallel, moniliform, chromatin threads which run spirally about the long axis.

A small pusule was noted at the anterior flagellar pore, and in one individual a very large posterior pusule extended from the posterior flagellar pore up to the nucleus. These pusules are filled with a pinkish fluid. No food balls were seen.

The color of this species has been found to be quite variable, possibly because of the results of previous ingested food. Dogiel (1906) gives to his figure a pale ochraceous color, located in chromatophore-like bodies. One individual seen by us had more of an amber-yellow tone, due also to chromatophore-like bodies distributed near the surface, principally dorsally, while in another the protoplasm was lavender grey with no trace of yellow or chromatophores. Minute glaucous green granules fill the periphery as cytolysis approaches. Dogiel figures lines of black pigment granules in the lower part of the hypocone below the girdle arranged as if along striae, though no such structural differentiations were to be detected in the surface plasma. In one case only did we find a detached pigment granule, and this lay anterior to the proximal end of the girdle.

Dimensions.—Length, 95–100$\mu$; transdiameter, 60–63$\mu$; diameter of nucleus, 31$\mu$; length of ocellus, 30$\mu$; of nematocysts, 14–22$\mu$.

Activities.—It is very active, rotating on its axis in anticlockwise direction with occasional brief reversals, and circling, under the cover glass, in clockwise circles. As it slows down the rotation ceases and the circles decrease in size until their diameter is only one to two times the length of the body. No discharge of the nematocysts has been noted either before or after cytolysis.

Occurrence.—A number of individuals were seen in the plankton at La Jolla, California, in July and August, 1917, but not recorded. Two were recorded from the hauls of a No. 25 silk net from 80 meters to the surface, 6 and 4 miles off La Jolla on July 20 and 27 respectively in surface temperatures of 20°5 C and 21°4 C respectively. A third was taken in a surface haul off the pier at the laboratory on August 4 in surface temperature of 21°5 C.

Dogiel (1906) records it as very abundant in surface plankton at times at Naples, Italy, during his investigations from May to the middle of July. Miss Lebour reports it as common in water samples from Plymouth Sound, England, in May and June in both free and encysted condition. These samples were taken 2.5 miles offshore from the surface and from 5 and 7 fathoms.

Comparisons.—The most striking difference between Dogiel's *P. armata* and our material of this species is in size. Our material has a length of 95$\mu$ and 100$\mu$, as determined by the measurement of two different individuals. His magnification is given as 850. If true, his organism was only one-half the size of ours, or 50$\mu$. A comparison of length, transdiameter, diameter of nucleus, lengths of nematocysts and of ocellus of his figure with our own reveals the fact that *all* these dimensions are but one-half those in our records, on the basis of his recorded magnification of 850. However, he also uses a magnification of 425 for certain other figures. If this magnification is applied to his figure the dimensions of the axis and organs noted above coincide almost exactly with those of our specimens. We regard this as an indication that the magnification given by him is probably an oversight and that the discrepancy in size may not exist. Miss Lebour (1917*b*) gives neither figure nor dimensions of her material. In proportions, girdle, sulcus, color, and number and arrangement of nematocysts our specimens agree closely with Dogiel's, except for the fact that his figure has reversed symmetry with the torsion and girdle running in the opposite direction to the normal and usual one. This appears to be due to error in his having drawn the structures of the lower surface upon the upper one. No case of critically determined, reversed symmetry is known to us in the Dinoflagellata, and this error of reversal of symmetry is one easily made in our experience.

This species shares with *Nematodinium partitum* the possession of nematocysts which have not been found elsewhere in the family. They are of the same type and size as in *Polykrikos*, although somewhat larger (10–15$\mu$) in this species than in *N. partitum* (6$\mu$ to 8$\mu$).

Its simple but concentrated ocellus, its nematocysts, and its considerable degree of torsion all mark it as one of the most specialized species of the genus and family.

### **Nematodinium partitum** sp. nov.

Plate 6, figure 68; text figures P, 2; MM; NN, 4

Diagnosis.—A medium sized species, ovoidal, length 1.7 transdiameters, girdle a descending left spiral of 1.25 turns, displaced 0.8 transdiameter, sulcus with both apical and antapical loops, its torsion 1.75 turns, ocellus of distributed type with numerous spherical lenses and diffuse black melanosome, situated far posteriorly; numerous nematocysts radiating from center. Length, 91$\mu$. Pacific off La Jolla, California, June, July.

Description.—The body is ovoidal with the broadest diameter slightly anterior to the equatorial region. The epicone and hypocone are subequal. The epicone is broadly rounded at the apex with a length above the anterior flagellar pore of 0.3 and distally on the right of the sulcus of 0.8 of the total length of the body. The hypocone is abruptly truncate at the right, is longer on the left side and broadly rounded there. It is traversed dorsally by the tip of the sulcus which sweeps around antapex in 0.66 of a turn and marks off a small, rounded terminal lobe.

The junction of the girdle and sulcus occurs at a point 0.3 of the total length from the apex. It curves around the body in a semicircle before taking a posterior direction, making 1.25 turns before meeting the sulcus at a point 0.13 of the total length from the antapex. It lies in a deep depression anteriorly, but less so distally. It is everywhere deeply impressed with overarching lips. The anterior flagellar pore opens at its anterior junction with the sulcus and the posterior pore just beyond its posterior junction. The transverse flagellum traverses 0.25 the total length of the girdle.

The sulcus invades the epicone in a broad curve, sweeping around nearly 0.75 of a turn in a deep trough which fades out distally. Below the anterior flagellar pore it describes 0.25 circumference in reaching its posterior junction with the girdle, beyond which it sweeps around the dorsal side of the hypocone in nearly a complete (0.75) turn of the descending spiral. On the dorsal side at this point the hypocone forms a deep, overhanging shelf on the proximal border of the sulcus, its distal border showing no perceptible protrusion.

The ocellus is situated below the distal end of the girdle and at the left of the sulcus and the posterior flagellar pore and extends in a dorsoventral direction. Its length is about 0.3 transdiameter. It consists of a distributed lens and a black amoeboid melanosome. The lens is composed of about fifteen to twenty greenish yellow, spheroidal, hyaline bodies packed in three layers, embedding the bases of the lens, and extending in long granular strands around them is the black pigment of the melanosome. Numerous black granules are scattered in rows along the borders of the girdle and the sulcus, especially posteriorly.

The nucleus is large, ellipsoidal, spherical, or pyriform and elongated posteriorly. It is situated near and anterior to the anterior flagellar pore. Fine chromatin strands traverse it, some in spiral directions. Its major and minor axes are 0.56 and 0.7 transdiameter in length respectively.

No pusules were observed. The cytoplasm is clear and very finely granular. A number of minute oil globules were present at the anterior end and a greater number in the posterior part. Scattered through the cytoplasm are numerous (15–20) nematocysts, greenish yellow in color. These are considerably smaller than those found in *N. armatum*, having a length of 5–8$\mu$ and a width of 2–3$\mu$. The majority take, in general, an anteroposterior direction. They are arranged roughly in three groups: one in the anterior part, one near the central region, and the third

posteriorly. Situated somewhat posteriorly is a large food body in which is found a group of radial rodlets radiating out from a common center and occupying apparently the center of the food body. These vary from 8–10$\mu$ in length and from 0.5–1$\mu$ in width and are pale greenish in color. The food mass consists of a small *Gymnodinium*, pale yellow in color. All evidence of internal structure had disappeared, leaving only an ovoidal outline and a broad girdle to distinguish it.

The color is a pale rose color distributed evenly throughout the cytoplasm near the periphery, leaving the central mass almost colorless. The animal was enclosed in a thin transparent cyst a little larger than the body and conformable to its contour.

Another encysted form (fig. P, 2), referred to *N. partitum* because of its ocellus and short rodlike bodies resembling nematocysts, was enclosed in a spheroidal, double-contoured, transparent cyst of nearly spherical form. When first observed it had an inner membrane closely applied to the spherical protoplasmic mass, but this later expanded somewhat irregularly till it met the outer membrane. In addition to the ellipsoidal nucleus and typical ocellus the enclosed protoplasmic sphere contained a yellow food ball and some scattered peg-shaped bodies, interpreted as nematocysts, the largest of which is about the size of the nematocysts of the individual of normal form.

The presence of cysts and of food balls in both of the individuals of this species that we have seen, and the abnormal (spherical) form of one of these, suggests that these may be digestion cysts, and that the form and contour may be more or less profoundly modified in this state. The individual upon which this description is based was, however, apparently normal in all important details.

Nutrition is undoubtedly holozoic and other species of Gymnodinioidae evidently fall victims to the voracity of this marauder. It is obvious that the *Gymnodinium* within the food vacuole is so large that its entrance into the cytoplasm of *Nematodinium* would severely stretch the intercingular part of the sulcus, close to which it lies, when it was ingested.

Dimensions.—Length, 91$\mu$; transdiameter, 52$\mu$; diameters of nucleus, 30–35$\mu$ and 25–28$\mu$; length of nematocysts, 5–8$\mu$.

Occurrence.—The individual figured was taken June 20, 1906, at La Jolla, California, with a No. 20 silk net in haul from 37 meters to the surface. Another encysted form was taken on July 9, 1917, with a No. 25 silk net in a haul from 80 meters to the surface in a surface temperature of 19°2 C.

Comparisons.—This species is a trifle smaller than *N. armatum*, has more numerous and smaller nematocysts, 5$\mu$ to 8$\mu$ as compared with 14$\mu$ to 22$\mu$, and a scattered ocellus instead of a concentrated one. The diffuseness of the ocellus is noteworthy as compared with the Pouchetiidae as a whole. No species of the family has more diffuse lenses and few exceed it in the diffuseness of its melanosome. The optical efficiency of the ocellus of this species judged by its position, multiplicity of lenses, and lack of coördination of these with the pigment must be of a low order.

### **Nematodinium torpedo** sp. nov.

Plate 11, figure 124; text figure NN, 3

Diagnosis.—A large species with elongate fusiform body, its length 2.9 transdiameters; girdle a descending left spiral of 2.25 turns; sulcus with nearly 2 turns, extending almost from apex to antapex; ocellus posteriorly located,

transverse, simple, with elongated lens, and small black melanosome; about 30 nematocysts grouped anteriorly. Length, 84μ. Pacific off La Jolla, California, August.

Description.—A remarkably specialized species with symmetrically fusiform body widest at the middle and tapering equally towards the two ends, with slightly convex contours between the furrows which notch its margins four times on either side. Its length is 2.9 its greatest diameter. The epicone and hypocone are subequal in size and volume. Each extends within 0.3 transdiameter of the end opposite to itself owing to the extreme torsion of the body. The apex is bluntly rounded, almost hemispherical in form, while the antapex is asymmetrically rounded, being longer on its left, as a result of the asymmetrical dislocation of the posterior end of the sulcus to the left.

The girdle forms a descending left spiral of 2.25 turns, growing steeper as it passes posteriorly from 5° at its proximal end to 50° at its distal junction with the sulcus. The interval of posterior displacement of the second turn is five times that of the first and the total distance of vertical displacement is 2.25 transdiameters of 0.78 total length. The furrow is deeply impressed with an overarching anterior lip. The sulcus makes nearly two complete turns. It extends anteriorly above the girdle towards the apex for 0.5 the distance, descends from its junction with the proximal end of the girdle in an ever steepening spiral to its posterior junction with the girdle within 0.3 transdiameter of the antapex. It is continued thence, not in a posterior course as usual in the Pouchetiidae, but in a continuation of the spiral which makes another 0.5 turn or more around the antapex beyond the posterior flagellar pore. This extension is indistinct. The transverse flagellum traverses, in the moribund state, only the anterior part of the girdle. The posterior flagellum arises from the pore at the posterior junction of girdle and sulcus and extends directly posteriorly, not in the spiral continuation of the sulcus around to the opposite side of the body.

The ocellus is 0.25 of the total length from the antapex, at the left of the posterior part of the intercingular sulcus, lies transversely and is directed to the left with its outer end somewhat protuberant. Its length is 0.6 transdiameter. It consists of an elongated, transparent, glaucous-blue lens with eight cupped lamellae and a very small, curved, bandlike melanosome across its adsulcal end. Its constituent parts are more correctly represented in figure NN, 3, than in the colored figure (pl. 11, fig. 124). No distinct colored core was detected.

The nematocysts are about thirty in number, arranged in two irregular circles around the anterior third of the body peripheral to the nucleus. They are all pointed anteriorly. They are yellowish green in color and in form are peg-shaped structures, 0.16–0.25 transdiameter in length, and their length is 2.5 to 4 times their greatest diameter which is anterior. There was no nuchal constriction delimiting a capitate end. The interior of the capsule is fluid-filled and contains the introvert consisting of the shaft and its spiral continuation coiled about it. On cytolysis of the body the nematocyst is discharged and forms a flat close spiral a little longer than the capsule.

The nucleus is elongated ellipsoidal, its major and minor axes being 0.9 and 0.5 transdiameter respectively in length. Its major axis coincides with that of the body. It lies just anterior to the middle of the body. No pusules were noted. Behind it is a spherical food vacuole containing an ochraceous food ball with two dark ochraceous chromatophores. A black spherical pigment grain lies near the apex and scattered about it are some smaller greenish oil globules, while larger highly refractive globules presumably of an oily nature lie near the antapex. The general color of the plasma is an exceedingly transparent, pale glaucous blue.

Dimensions.—Length, 83μ; greatest transdiameter, 29μ; length of nucleus, 28μ; of ocellus, 18μ; of nematocysts, 5–8μ.

Occurrence.—One individual taken in a haul of a No. 20 silk net in haul No. 1395, June 24, 1907, from 100 meters to the surface 2 miles off La Jolla, California, in latitude 32° 53′.1 N, 117° 17′.3 W, in surface temperature of about 16°.5 C.

Comparisons.—This species is built for rapid locomotion, as shown by its shape and its furrows. Its nematocysts are small as in *N. partitum*, and it shares with the other species in the genus the posterior location and transverse direction of the ocellus, the continuation of the spiral course of the sulcus beyond the posterior flagellar pore on to the dorsal side of the antapex, and the clustering of the nematocysts about the nucleus. It is highly specialized in form, in grouping of the nematocysts and integration of the lens.

CHAPTER XIX

# POUCHETIIDAE: POUCHETIA

## **POUCHETIA** Schütt emend.

Text figures OO–QQ

*Pouchetia* Schütt (1895), in part, pp. 168–170, pl. 26, figs. 92, 94; pl. 27, figs. 97–99; (1896), p. 6, fig. 8.

*Gymnodinium,* Pouchet (1885*a*), in part, pp. 38–39, 85, pl. 2, fig. 1; (1885*b*), pp. 529-531, 534, pl. 3, fig. 4; (1887), pp. 96–97, 112, pl. 10, fig. 1.

*Pouchetia,* Delage and Hèrouard (1896), in part?, p. 384, fig. 668.

*Pouchetia,* Paulsen (1908), in part, pp. 105–106, figs. 146, 148.

*Pruchetia,* Lohmann (1908), p. 369. *Lapsus.*

### Diagnosis

Pouchetiidae with an ocellus located at the left of the intercingular sulcus; no posterior prod; girdle a descending left spiral of 1.15 to 2 turns; sulcus with torsion of 0.25 to 1.75 turns of a descending left spiral, its apical loop with from 0 to 1.5 turns, and its antapical loop sometimes attaining 1 turn. No paracingular lines. Ocellus with red or black pigment mass with red, brown, yellow, or colorless central core; lens hyaline, laminate, or of appressed parts or segments. Nucleus usually anterior to ocellus; perinuclear membrane rarely present; moniliform chromatin threads distinct. Pusules, if present, opening anteriorly into the anterior flagellar pore or posteriorly into the posterior. No nematocysts; surface striae rarely present; plasma generally highly colored; scattered melanin or other pigment granules sometimes present. Holozoic nutrition; encystment in thin-walled membrane frequent. Length, 32-141$\mu$. All marine, eupelagic and from warm temperate or tropical seas; 20 species known.

### Organology

*Pouchetia* has about as much torsion of the body as *Cochlodinium*, but with this marked difference, namely, that the sulcus above the proximal and below the distal ends of the girdle is itself continued in a spiral course which may equal or even exceed the amount of torsion within the intercingular part of that organ, whereas in *Cochlodinium* the torsion is mainly in the intercingular region and the apical and antapical loops are never extended to the amount of so much as 0.5 turn. In *Pouchetia,* on the other hand, either or both of these loops may make as much as a full turn about the body, as for example in *P. violescens* (fig. OO, 1). The apical loop may even make as much as 1.5 turns, as in the species cited. When, however, the girdle of *Pouchetia* has two full

turns, as in *P. purpurescens* (pl. 8, fig. 84) and *P. fusus* (fig. PP, 1), these terminal loops of the sulcus are lacking and the ends of the sulcus have little or no torsion, thus resembling *Cochlodinium.*

The length and torsion of the sulcus are intimately correlated with the length, proportions, and constriction of the body, and the terminal loops tend to increase the asymmetry of the species of this genus as compared with more symmetrical species of *Cochlodinium* (cf. figs. GG and OO).

The presence of an antapical loop encircling the antapex *below* the point of emergence of the posterior longitudinal flagellum accentuates the asymmetry of the antapical region (see *P. maculata*, pl. 11, fig. 119), and provides the basis for a progressive mobility of this region within *Pouchetia*, which renders this territory very difficult to examine and portray adequately and correctly. It also affords the earlier stages in the evolution of the remarkably active and extraordinay prod, or tentacle, of *Proterythropsis* and *Erythropsis.*

It seems probable that the apical loop performs a like function for the apex, which in *Erythropsis* is invaded by the anterior end of the sulcus and is somewhat labile. In *P. violescens, P. juno,* and *P. atra* (figs. OO, 1, 3; PP, 5) modifications of the apical region are brought about by this apical loop of the sulcus.

The ocellus in *Pouchetia* has all stages in the integrative process of combining scattered pigment spherules into a compact mass enveloping the base of the lens, and in a correlated combination of separate hyaline spheres into a spheroidal laminate lens.

This process is clearly one of integration. The evidence for this conclusion lies in the fact that those species (subgenus *Pouchetia*) with the diffuse nonintegrated type of ocellus, such as *P. alba* (fig. PP, 8), *P. poucheti* (fig. PP, 4), *P. schuetti* (fig. PP, 10), and *P. purpurata* (fig. PP, 3), are not highly specialized in other structural features. They are nearer to *Gymnodinium* and *Cochlodinium* than are the species with the integrated ocellus. They have less torsion in the girdle and sulcus, and both *P. alba* and *P. poucheti* are almost colorless (pl. 11, figs. 121, 125), being lightly tinged with yellow and blue respectively, while *P. schuetti* and *P. purpurata* with a more concentrated type of ocellus reach the red end of the spectrum. *P. fusus* is yellow, has the *Cochlodinium* type of torsion, without terminal loops in the sulcus, and its ocellus has a unique ringlike melanosome binding together a bipolar lens.

The group of species (subgenus *Pouchetiella*) with more highly integrated lens and melanosome also has within it various stages in the later phases of the integrative process. In fact the distinctions between the two groups are not clearly defined. The highest stage of integration results in a spheroidal lens with concentric laminae, with one face buried in a black pigment mass or melanosome which is also spheroidal or hemispheriodal and contains within its center, in contact with the surface of the lens, a highly colored sensory (?) core. Such ocelli are to be found in the highly specialized species such as *P. juno, P. violescens, P. maxima,* and *P. striata* (fig. OO). They are usually median in position and have their axes horizontal or 45° from the horizontal and directed

to the left anteroventrally or anterosinistrally. They are thus by structure and position more highly specialized for their function than the looser aggregates of the more primitive species of *Pouchetia*, and than the less integrated ocelli of *Pouchetiella*, such as *P. maculata* and *P. voracis* (figs. PP, 12, 2). In these less integrated types the ocellus is usually farther posterior, smaller, both relatively and absolutely, and may have an elongated lens more or less lobed or transversely laminated as in *P. voracis* (fig. PP, 2), *P. atra*, and *P. maculata* (pl. 11, figs. 126 and 119).

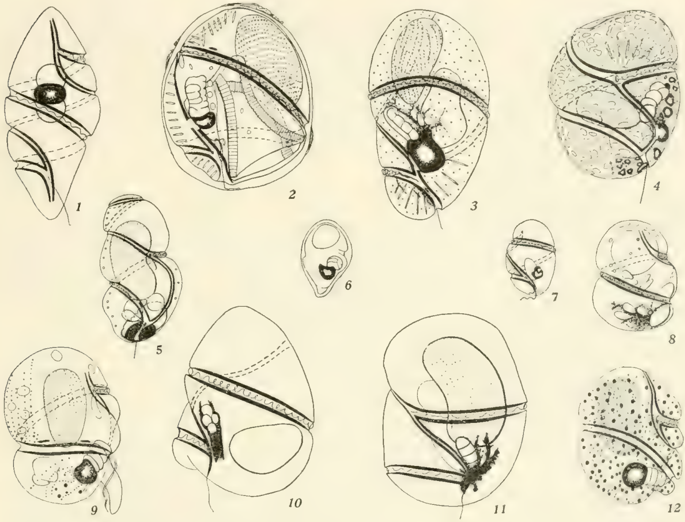


Fig. PP. *Pouchetia* Schütt and *Proterythropsis* gen. nov. 1. *Pouchetia fusus* Schütt. After Schütt (1895, pl. 26, fig. $94_1$). 2. *P. voracis* sp. nov. 3. *P. purpurata* sp. nov. 4. *P. poucheti* sp. nov. 5. *P. atra* sp. nov. 6. *P. parva* Lohmann. After Lohmann (1908, pl. 17, fig. 23). 7. *P. panamensis* Kofoid. After Kofoid (1907, pl. 1, fig. 7). 8. *P. alba* sp. nov. 9. *Proterythropsis crassicaudata* sp. nov. 10, 11. *Pouchetia schuetti* (Schütt). After Schütt (1895, pl. 26, figs. $92_{3,\,10}$). 12. *P. maculata* sp. nov. × 500.

The nucleus of *Pouchetia* always has distinct beaded, chromatin threads and has not been found with the perinuclear membrane surrounding a hyaline area about the regular nuclear contents. It is usually located anterior to the ocellus. The exception to this relation, seen in *P. compacta* (fig. PP, 9), as oriented by Schütt (1895), may be due to an incorrect interpretation as to the anterior and posterior ends of the organism.

The genus *Pouchetia* shares with *Cochlodinium* the relative freedom from longitudinal striae upon the surface of the body. These striae are common in *Gyrodinium* and *Gymnodinium*, but are not associated in *Pouchetia* with primitive or generalized species. Only three species have striae, *P. striata, P. violescens*, and *P. maxima* (figs. OO, 8, 1, 2), all highly specialized forms. Suggestions of an underlying but ordinarily invisible linear organization of the cytoplasm appear in the faintly linear grouping of pigment granules in *P. maculata* (pl. 11, fig. 119), and the linear aggregates of pigment in *P. violescens* (pl. 11, fig. 118).

The color of the cytoplasm in *Pouchetia* is remarkably diversified, changeable in tone and in aggregation, and probably subject to considerable modifications as a result of internal physiological states and stages of metabolism (cf. figs. 118, 120, pl. 11). It may be diffuse as in *P. rubescens* (pl. 8, fig. 90), *P. purpurescens* (fig. 84), *P. purpurata* (fig. 87), and *P. voracis* (fig. 89); or in spheroidal aggregates as in the black granules of *P. maculata*, or the greenish flecks of *P. poucheti*.

Nearly the whole range of colors of the spectrum is to be found within the species of this genus, but most of them near the red end. *P. violescens* (pl. 11, fig. 118), *P. juno*, and *P. maxima* (pl. 6, fig. 61) lie near the violet end, exhibiting tones of violet and lavender. *P. poucheti* (pl. 11, fig. 125) is bluish green, *P. atra* (fig. 126) somewhat greenish, *P. alba* (fig. 121) faintly tinged with pale yellow, *P. fusus* and *P. parva* are ochraceous, and the remaining twelve species exhibit various shades of red, grading from the darker purples of *P. purpurata* and *P. purpurescens* to the rosy tint of *P. voracis*. While there is no exact and uniformly graded parallelism between the colors of the species of *Pouchetia* arranged in the scale of the spectrum from violet to red and the progressive structural specialization of these species, there is, nevertheless, a sufficient difference to justify the conclusion that pigment formation is a feature of progressive specialization in these organisms, passing from the faintly tinged bluish green to the red and black colors, and that this is accompanied by structural specializations of the ocellus, sulcus, and girdle. The evidence is as follows: (1) the simplest species with least integrated ocellus and most *Gymnodinium*-like furrows, *P. alba* and *P. poucheti* are faintly tinged with bluish green and yellow; (2) all the rose-red species, *P. compacta, P. panamensis, P. polyphemus, P. rosea* (Pouchet), *P. rubescens, P. striata, P. subnigra*, and *P. voracis*, and the reddish-black *P. maculata* have well integrated ocelli, and a high degree of complexity of girdle and sulcus. The two ochraceous species, *P. fusus* and *P. parva*, are less specialized. There remains a group of purplish species, *P. purpurata, P. purpurescens*, and *P. schuetti*. The first two of these are highly specialized, the last less so. The two violet-lavender species, *P. violescens* and *P. juno*, are highly specialized large species, and as such do not exhibit the simplicity in structures shown in the general trend of the genus at the violet end of the spectrum. The preponderance of evidence, however, suggests a

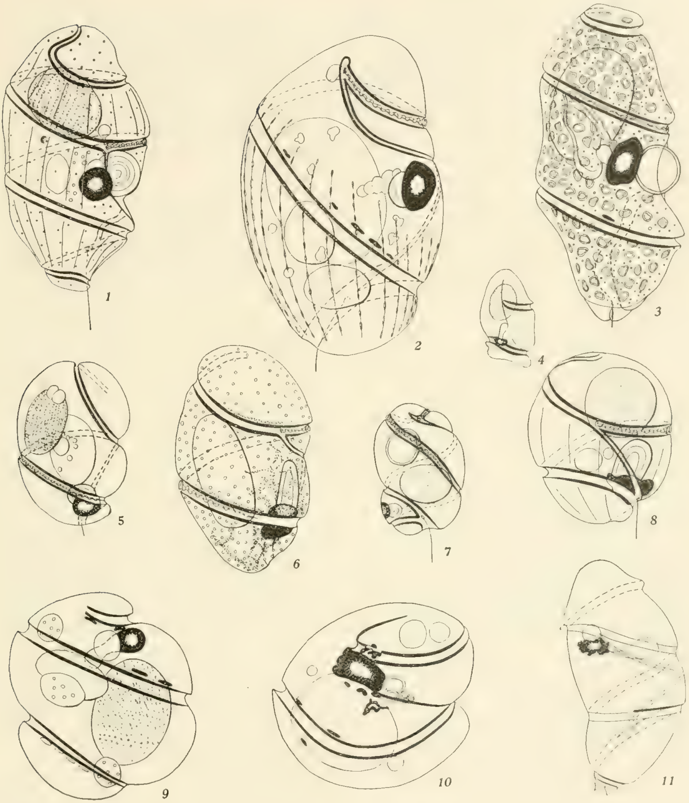

Fig. OO. *Pouchetia* Schütt. 1. *P. violescens* sp. nov. 2. *P. maxima* sp. nov. 3. *P. juno* Schütt. After Schütt (1895, pl. 37, fig. $99_1$). 4. *P. rosea* (Pouchet). After Pouchet (1885*b*, pl. 26, fig. 1). 5. *P. rubescens* sp. nov. 6. *P. subnigra* sp. nov. 7. *P. purpurescens* sp. nov. 8. *P. striata* sp. nov. 9. *P. compacta* Schütt. After Schütt (1895, pl. 27, fig. $97_1$). 10. The same. After Schütt (1895, pl. 27, fig. $97_2$). 11. *P. polyphemus* (Pouchet). After Pouchet (1885*b*, pl. 26, fig. 3). × 500.

correlation between pigment formation and structural specialization within the genus *Pouchetia*.

Many if not all the species of this genus are holozoic in nutrition. The evidence for this lies in the presence of food balls within food vacuoles in the cytoplasm, the accumulations of the products of metabolism in the form of oil globules, vacuoles, refractive rodlets and platysomes in the central or peripheral plasma, and the presence of recognizable organisms within the food vacuoles in a few cases. For example, *P. voracis* (fig. PP, 2) was found with the entire theca of a species of *Peridinium* within it.

It is possible that the small *P. parva* is holophytic, but the only basis for this conclusion is its ochraceous color. It is evident, however, that Lohmann's figure is quite diagrammatic and wholly inadequate to determine this matter. There is no evidence that any of the other species have any chlorophyll or xanthophyll of their own. The yellow bodies found within them appear in all cases to be in food balls.

The intercingular sulcus is probably the mouth and it is not impossible that the two pusules may represent remnants of areas of ingestion. The capture of organisms and their ingestion have not been observed. The ejection of undigested remnants has been watched in *P. maxima*. The antapex is rent open, forming a protoplasmic skirt, and the fecal mass is extruded (pl. 6, fig. 61) from its opening. The resulting modifications, which are temporary, are one cause of the variability of the antapical region of this genus. It is also obvious (fig. PP, 2) that the presence of large food masses may distort the contour or even push aside ocellus and nucleus.

The wide prevalence of the formation of cysts in *Pouchetia* is correlated with this holozoic nutrition. Individuals within cysts frequently exhibit food balls or metabolic products (fig. P.) Such cysts are their digestion cysts temporarily formed for a quiescent period of appropriation of a relatively large volume of food. We have no evidence of binary fission within cysts in *Pouchetia*.

The cyst forms as a pellicle on the surface of the plasma and is expanded by the fluid accumulating within it by osmosis. The agency of the plasma, especially along the sulcus, in this process is suggested by the more rapid distension of the membrane immediately over this organ.

## Distribution

Species of *Pouchetia* have been reported principally from warm temperate and tropical seas and only from more northerly waters receiving warm currents from these warmer regions. It is unfortunate that Schütt's monograph (1895) gives no clue to the precise source of his species, *P. compacta, P. fusus, P. juno,* and *P. schuetti* nom. sp. nov. (= *P. rosea* (Pouchet) Schütt). They are presumably from the Bay of Naples or from collections of the Plankton Expedition in the Atlantic. Pouchet's material of *P. polyphemus* and *P. rosea* came from

Concarneau on the west coast of France within the influence of the Gulf Stream. The same influence accounts for the more northerly records of Miss Lebour (1917*b*) of *P. fusus* at Plymouth, England, and Pouchet's isolated record of *P. polyphemus* in Dyrefjord, Iceland, and probably also for the records of *P. rosea* in the North Sea and Cattegat off the coasts of Denmark by Ostenfeld (1913). On the other hand, *P. parva*, recorded thus far both by Lohmann (1908, 1911) in the Baltic at Kiel and by Miss Lebour at Plymouth, may be more of a northern and neritic species.

The only species recorded thus far from the Mediterranean are *P. rosea* (Pouchet) by Pavillard (1905) at Cette and by Schröder (1900) from Naples. The latter record may be for *P. schuetti*. The only species thus far reported from the Pacific is *P. panamensis* by Kofoid (1907*a*) from the Bay of Panama.

To this single record for the Pacific we add in this paper from the plankton off San Diego and La Jolla, California, the following species previously described: *P. rosea* (Pouchet), *P. juno* Schütt; and twelve new ones as follows: *P. alba, P. atra, P. maculata, P. maxima, P. poucheti, P. purpurescens, P. purpurata, P. rubescens, P. striata, P. subnigra, P. violescens,* and *P. voracis.*

## Historical Discussion

This genus was established by Schütt (1895), who figured *P. compacta* (called *P. contorta* in his explanation of plates), *P. fusus, P. juno,* and *P. rosea* (Pouchet). His *P. rosea* is, however, not Pouchet's *Gymnodinium polyphemus* var. *roseum* (1887, pl. 10, fig. 1), but a distinct species, *P. schuetti* nom. sp. nov. He also figured *P. cochlea* and *P. cornuta*, both of which belong to *Erythropsis*. He later (1896) characterized the genus *Pouchetia* and established *P. fusus* as its type (monotypic). Pouchet in a series of papers (1884, 1885*a*, 1885*b*, 1886*a*, 1886*b*, 1887) called attention repeatedly to the ocellate forms of the dinoflagellates. His figures are usually very incomplete and inadequate and his conception of the species he dealt with both inconstant and confused. He regarded them all as species of *Gymnodinium*. This lack of precision is due in part to the difficulties in working with these delicate organisms, their small numbers, and to the newness of the field.

We regard his "*Peridinium* voisin de *Gymnodinium spirale*" (1885*a*, p. 85, pl. 2, fig. 1) as a *Pouchetia*, but indeterminable until some one finds the species again. His *G. polyphemus* (1885*b*, p. 534, pl. 26, fig. 3) is a *Pouchetia*, but different from his *G. polyphemus* var. *roseum* (1887, pl. 10, fig. 1), which is *P. rosea* (Pouchet), but not *P. rosea* (Pouchet) Schütt (1895), which is *P. schuetti* nom. sp. nov. His *G. polyphemus* var. *nigrum* (1887, pl. 10, fig. 2), which Lemmermann (1899) placed in *Pouchetia*, we transfer to the new genus *Protopsis*. In 1907 Wright added *P. ochrea* to the genus. This we transfer to *Protopsis*. In the same year Kofoid described *P. panamensis*, and in 1911 Lohmann added *P. parva*, which by a slip of pen became (1911, p. 369) *Pouchetia paron*. The same author earlier (1908, p. 152) introduced a *nomen*

*nudum*, *Pouchetia baltica*. In 1906 Dogiel described *P. armata*, a species with nematocysts. This we transfer to *Nematodinium* gen. nov. Dogiel also by erroneous citation adds *Gymnodinium polyphemus* var. *magna* to the *nomina nuda* referable to *Pouchetia*.

Our emendations to the genus exclude from it those species without torsion (*Pouchetia nigra* (Pouchet) Lemmermann and *P. ochrea* Wright). These we place in *Protopsis* gen. nov. We also exclude all ocellate types with paradinial lines and posterior prod (*Pouchetia cornuta* and *P. cochlea* of Schütt, 1895) which belong in *Erythropsis*, and one new ocellate species without paradinial lines and with rudimentary prod which is the type species (*crassicaudata*) of a new genus *Proterythropsis*. All ocellate species with nematocysts we place in *Nematodinium* gen. nov. This transfers Dogiel's (1906) *Pouchetia armata* to *Nematodinium,* to which we add two new ocellate species, *N. partitum* and *N. torpedo*.

To the residue of six previously described species remaining in *Pouchetia*, to wit, *P. fusus* Schütt, *P. compacta* Schütt, *P. juno* Schütt, *P. panamensis* Kofoid, *P. polyphemus* (Pouchet) emend., *P. rosea* (Pouchet) emend., we add twelve new species from the plankton of the Pacific off La Jolla, California, as follows: *P. alba, P. atra, P. maculata, P. maxima, P. poucheti, P. purpurescens, P. purpurata, P. rubescens, P. striata, P. subnigra, P. violescens,* and *P. voracis*, and a thirteenth, *P. schuetti* nom. sp. nov., based on Schütt's (1895) figures of *P. rosea* (Pouchet).

## SUBGENERA OF **Pouchetia**

### Subgenus 1. **Pouchetia** subgen. nov.

Ocellus not concentrated or integrated; lens in two or more parts, scattered or arranged in one row; melanosome in the form of a diffuse network of scattered disconnected spherules. Type, *P. fusus* Schütt. This subgenus includes besides the type, *P. alba* sp. nov., *P. poucheti* sp. nov., *P. purpurata* sp. nov., and *P. schuetti* nom. sp. nov.

### Subgenus 2. **Pouchetiella** subgen. nov.

Ocellus integrated; lens spheroidal, laminate, or composed of closely applied segments and elongated, massive melanosome, not sending out stout pseudopodia and not parted into spherules, closely applied to the base of the lens and usually containing a red or brown sensory core. Type species, *P. violescens*. This subgenus contains in addition to the type the following species: *P. atra* sp. nov., *P. compacta* Schütt, *P. juno* Schütt, *P. maculata, P. maxima* sp. nov., *P. panamensis* Kofoid, *P. parva* Lohman, *P. polyphemus* (Pouchet), *P. purpurescens* sp. nov., *P. rosea* (Pouchet) emend., *P. rubescens* sp. nov., *P. striata* sp. nov., *P. subnigra* sp. nov., and *P. voracis* sp. nov.

## KEY TO THE SPECIES OF **Pouchetia**

1. Ocellus diffuse, pigment scattered or amoeboid, lens in several pieces (subgenus **Pouchetia**) .......... 2
1. Ocellus integrated, pigment mass compact, lens single (subgenus **Pouchetiella**) .......... 3
2. Melanosome ring-shaped, lens bipolar .......... **fusus** Schütt
2. Melanosome not ring-shaped .......... 4
4. Plasma reddish or purplish .......... 5
4. Plasma greenish or yellowish .......... 6
5. Plasma rosy, antapical region not contracted, torsion 0.25 turn .......... **schuetti** nom. sp. nov.
5. Plasma purplish, antapical region contracted, torsion 0.50 turn .......... **purpurata** sp. nov.
6. Plasma pale yellowish, ocellus posterior, body wider posteriorly .......... **alba** sp. nov.
6. Plasma bluish green, ocellus median, body ellipsoidal .......... **poucheti** sp. nov.
3. Pigment mass rosy, not of melanin .......... **rosea** (Pouchet) emend.
3. Pigment mass with more or less melanin .......... 7
7. Large species, over $100\mu$ in length, ocellus median, horizontal .......... 8
7. Less than $100\mu$ in length, ocellus posterior, or if median not horizontal .......... 9
8. No long apical loop of sulcus, faint striae posteriorly, plasma lavender.......... **maxima** sp. nov.
8. Apical loop of at least 1 turn .......... 10
9. Ocellus far anterior .......... **compacta** Schütt
9. Ocellus not premedian .......... 11
10. Apical loop of 1.5 turns, surface with longitudinal striae, plasma violet .......... **violescens** sp. nov.
10. Apical loop of 1 turn, surface with rounded platysomes, no striae .......... **juno** Schütt
11. Longitudinal striae present, body rotund .......... **striata** sp. nov.
11. No longitudinal striae .......... 12
12. Length more than 2 transdiameters, large species .......... **polyphemus** (Pouchet) emend.
12. Length less than 2 transdiameters .......... 13
13. Small species, less than $50\mu$ in length .......... 14
13. Length more than $50\mu$ .......... 15
14. Plasma rosy .......... **panamensis** Kofoid
14. Plasma ochraceous .......... **parva** Lohmann
15. Apical loop of 1.5 turns, ocellus far posterior .......... **atra** sp. nov.
15. Apical loop, if present, with less than 1.5 turns, ocellus not at postmargin .......... 16
16. Girdle displaced at least 0.75 total length of body .......... **purpurescens** sp. nov.
16. Girdle displaced less than 0.75 total length .......... 17
17. Length more than 1.5 transdiameters, lens elongated, granular black pigment strands .......... **subnigra** sp. nov.
17. Length not more than 1.5 transdiameter, pigment not in amoeboid strands .......... 18
18. Diffuse rosy pigment throughout body .......... 19
18. Black pigment scattered in peripheral spherules .......... **maculata** sp. nov.
19. Ocellus median, displacement more than 0.5 length of body .......... **voracis** sp. nov.
19. Ocellus posterior, displacement less than 0.5 length of body .......... **rubescens** sp. nov.

### **Pouchetia alba** sp. nov.

Plate 11, figure 121; text figure PP, 8

DIAGNOSIS.—Small species with ovoidal body, enlarged posteriorly, its length 1.3 transdiameters; girdle 1.5 turns around body, displaced about 0.6 total length of body; torsion 0.5 circumference; ocellus irregular, compound, situated far posteriorly; lens double; amoeboid melanosome and scattered black pigment. Length, 45μ. Pacific off La Jolla, California, July.

DESCRIPTION.—The body is small, ovoidal with the longest transdiameter posterior to the middle of the body and nearly circular in cross-section. The epicone is somewhat smaller than the hypocone, is symmetrically rounded near the apex, and has a length of about 0.3 of the total length of the body on the left and of about 0.88 on the right side of the sulcus. The hypocone is broadly rounded, flattened on the antapex and deeply excavated on the ventral side by the posterior end of the sulcus.

The girdle joins the sulcus at a point distant from the apex 0.3 of the length of body, sweeps around the body posteriorly 1.5 times and joins the sulcus distally 0.2 of the total length from the antapex. The anterior flagellar pore is found at the proximal junction of the girdle and sulcus, and the posterior flagellar pore slightly beyond the distal junction on the opposite face of the body from the anterior pore. The transverse flagellum traverses nearly the whole length of the girdle.

The sulcus begins midway between the anterior flagellar pore and the apex without a terminal loop, curves regularly around the body 0.5 its circumference and is continued beyond the posterior flagellar pore to near the antapex as a deep trough.

The ocellus is situated at the right of the distal end of the sulcus and the posterior flagellar pore, and is directed obliquely anteroventrally. It has a compound, colorless lens, composed of two ovoidal masses of hyaline material with concentric lines only faintly indicated. It is crossed by the distal end of the girdle. The lens is large, being 0.3 the total length of the body in length, its cross-diameter being 0.3 its own length. The two component moieties are obliquely flattened against each other. Adjacent to the base of the lens is a small, spheroidal, denser part of the black melanosome surrounding a very minute central core. Around this, partially covering the posterior part of the lens and scattered through the distal third of the hypocone, is a loose mass of black granules which exhibit amoeboid changes of position. A detached mass of black pigment and several granules lie near the anterior flagellar pore.

The nucleus is situated in the epicone, an almost spherical body with a diameter of 0.7 transdiameter. Numerous chromatin strands traverse it in an anteroposterior direction.

The pusules were evident. The cytoplasm is finely granular and transparent, with few alveoli or large granules present. Small greyish refractive bodies were situated in the epicone with several large oil globules and greenish food vacuoles posteriorly. The surface of the body lacks striae or other markings and there are no peripheral vacuoles. The color is a pale viridine yellow diffused throughout the plasma.

DIMENSIONS.—Length, 45–50μ; transdiameter, 30–35μ; dorsoventral diameter, 35μ; nucleus, 30μ.

ACTIVITIES.—A normally active individual moves anticlockwise in large circles, with rapid, slightly jerking motions.

OCCURRENCE.—Two individuals were seen. These were taken in a No. 25 silk net in the Pacific Ocean off La Jolla, California, on July 12 and 17, 1917. The hauls were made from a depth of 80 meters to the surface and in a surface temperature of 20°5 C.

COMPARISONS.—*Pouchetia alba* is the least differentiated member of the subgenus *Pouchetia*. Its primitive stage of development is indicated by the very slight coloration and its location in the yellow-green part of the spectrum, by the slight torsion of the sulcus and relatively small amount of displacement of the girdle. The intercingular region is equivalent to that found in the genus *Gyrodinium*. The ocellus is also in the diffuse stage with little evidence of functional and structural integration. The two segments of the lens are not fused, the pigment mass is small in amount, scattered in amoeboid processes away from the lens, is not applied closely to any large area of the lenses and contains no red core. Neither the adjustment of lens and pigment nor the location and direction of the axis of the ocellus are suggestive of functional efficiency. In these particulars this species is most nearly approached by *P. poucheti* (fig. PP, 4).

## **Pouchetia atra** sp. nov.

Plate 11, figure 126; text figure PP, 5

DIAGNOSIS.—Body ovoidal; length, 2 transdiameters; girdle a descending left spiral of 1.6 turns, displaced nearly 1 transdiameter; sulcus with apical loop of 1.75 turns, its torsion 2 turns; ocellus posterior, concentrated; lens elongate; black, amoeboid melanosome with red central core. Length, 64$\mu$. Pacific off La Jolla, California, July.

DESCRIPTION.—The body is rather slender, ovoidal with the widest diameter below the equatorial zone. It is deeply constricted by the girdle and the sulcus. The epicone considerably exceeds the hypocone. The length of the epicone above the anterior flagellar pore is 0.4, and at its distal extremity 0.85 of the total length of the body. It contracts distally, its apex is rounded, and its sides are deeply grooved by the sulcus which makes 1.75 turns around it. The hypocone is slightly broader than the epicone and has proximal and distal lengths of 0.6 and 0.15 respectively of the total length of the body. It is slightly asymmetrical and more convex anteriorly. The antapex is asymmetrically rounded, being longer at the right. The sulcus makes but a shallow groove down the left face, ending at or near the antapex. There is no antapical process and no sulcal notch.

The junction of the sulcus and girdle is located 0.4 of the total length of the body from the apex. It sweeps around the body in a descending left spiral as a deep trough with bulging, overhanging borders, making 1.6 turns before its posterior junction with the sulcus 0.15 of the total length from the antapex. The anterior flagellar pore opens at its anterior junction with the sulcus and the posterior flagellar pore at its posterior junction. The transverse flagellum traverses 0.8 of its length.

The sulcus takes origin near the apex and forms a descending left spiral of 1.75 turns before reaching the anterior flagellar pore, beyond which it makes a sweeping curve to the right, descends to the posterior junction with the girdle and thence posteriorly in almost a straight line to the antapex. Its narrow channel is more deeply embedded anteriorly and on the left face of the epicone than it is elsewhere, and especially toward the antapex.

The ocellus is relatively large and is situated at the extreme posterior end. It is at the left of and behind the sulcus, directed obliquely anterosinistrally about 45° from the main axis. The lens is of the imperfectly concentrated type and shows a marked tendency toward the

diffuse, having the distal border imperfectly lobed and slender strands of granular pigment distributed on the lens. It is elongated, 0.6 transdiameter in length, with a width of 0.5 its own length. It is circular in cross-section and greenish blue at the distal end, changing to yellow ochre towards the melanosome. Ventroposterior to the lens and partly embedding one side of it is the melanosome. This is large, 0.3 transdiameter in length. It is composed of black pigment with a red core. Streaming out from it are amoeboid strands of black granules, one of which closely invests the right border of the lens, another passing over its dorsal face.

The nucleus is large, elongate reniform, and occupies the central area of the body with its major axis longitudinal. Rather coarse strands of chromatin curve around its major axis, about fourteen on one face. Its length is 1.1 and its width 0.5 transdiameters. A small, pink club-shaped pusule opens at the anterior and another at the posterior flagellar pore.

The cytoplasm is rather coarsely granular with a few greenish oil droplets peripherally located in the median and posterior regions. A large, blue-green food mass is found in the posterior part near the ocellus.

The color is bluish green, diffused throughout the cytoplasm. The organism was enclosed in a thin transparent cyst slightly larger than the body and conformable to its contour. An unusual condition was noted in that a few bluish-green oil granules were present against the inner surfaces of the cyst outside of the body. This species was found in both the encysted and free state. The constrictions of girdle and sulcus were deeper in the encysted stage and the ventral arching more pronounced in the free state. The cyst wall was rather heavy and transparent, adhered to the glass, and was rather closely applied in the two cysts observed.

DIMENSIONS.—Length, 60–64$\mu$; transdiameter, 25–32.5$\mu$; axes of nucleus, 36$\mu$ (18) and 15$\mu$ (10); length of lens, 19$\mu$.

The unusual size of the nucleus figured was evidently due to the approach of division, the other forms seen having a much smaller ellipsoidal nucleus, as may be seen from the measurements in parentheses.

OCCURRENCE.—Three individuals were taken July 23, 1917, 6 miles off La Jolla, California, with a No. 25 silk net in a haul from 80 meters to the surface and in a surface temperature of 20°8 C.

COMPARISONS.—*Pouchetia atra* is on the borderline between the two subgenera *Pouchetia* with diffuse ocellus and *Pouchetiella* with the concentrated type. Its melanosome is only slightly lobed and its amoeboid streamers are feebly developed. The lens is also elongate and slightly lobed and not fully integrated by location into a typical axial relation to the melanosome. This lack of complete concentration it shares with certain other species with posterior ocellus such as *P. alba*, *P. maculata*, and *P. schuetti*, and with several species with median ocellus such as *P. maxima*, *P. poucheti*, and *P. purpurata*. The ocellus is farther posterior in *P. atra* than in any other species and exhibits one of the later steps in the evolutionary integration of this organ towards the concentrated type. The ocellus in the free individual had a slightly more anterior position and had more of an anterior direction of its optical axis, much as in *P. purpurata*. It is possible that the pressure of the food ball in the individual figured (pl. 11, fig. 126) is responsible for the extreme posterior position of its ocellus and for the discoloration of its lens.

## Pouchetia compacta Schütt

Text figures OO, 9, 10

*Pouchetia compacta* Schütt (1895), pp. 96, 97 (pl. 27, figs. $97_{1-7}$, by citation only).
*P. contorta* Schütt (1895), pp. 169, 170, pl. 27, fig. $97_{1-7}$.
*P. contorta*, Lemmermann (1899), p. 360.

DIAGNOSIS.—A large species; body very rotund, length 1.1 transdiameters; girdle a descending left spiral of 1.5 (?) turns, displaced about 0.5 (?) transdiameter; sulcus with about 1.25 turns; ocellus anteroir, subhorizontal, concentrated, elongate lens (?), black, amoeboid melanosome; rosy vacuoles. Length 91μ. Plankton Expedition, Atlantic (?), or Bay of Naples.

DESCRIPTION.—This is based on Schütt's (1895, pl. 27, figs. $97_{1-7}$) figures, explanation of figures and brief textual references. Body very rotund (probably much contracted), its longitudinal axis only 0.1 greater than its transverse axis. The epicone is broadly rounded, somewhat flattened at the apex, and deeply constricted at the left side. The hypocone is asymmetrically rounded, the distal end of the sulcus (?) deeply notching it on the left side. The sulcus is only faintly indicated in the second one of Schütt's figures (text fig. OO, 10), thus making uncertain the definite measurements of regions related to that structure. From these indications the anterior point of junction of the girdle and sulcus would seem to be just above and to the right of the ocellus in the body. From that point it passes posteriorly over the notch in the melanosome (text fig. OO, 10) and joins the girdle again distally at a point on the opposite face of the body from that shown in the figure, then sweeps around the hypocone in the deep trough shown in the lower part of text figure OO, 9, as the antapical loop. This seems to be the only possible interpretation to be placed on the two figures given by Schütt, and the description given herewith is based on that assumption. If this be the true interpretation it makes the epicone considerably smaller than the hypocone, with approximate lengths from the apex to the proximal and to the distal extremities of the epicone of about 0.2 and 0.6 of the total length respectively.

The girdle begins apparently at a point just above the ocellus, passes around the body in a horizontal semicircle before changing its course to a steep spiral in the dorsal side, flattening again prior to its posterior connection with the sulcus. It thus makes nearly 1.5 turns around the body before meeting the girdle distally on the left face of the organism, with a total displacement of about 0.5 transdiameter. It forms a broad, rather deep channel throughout its course with the lips smooth and rounded. No pores or flagella have been figured.

The sulcus takes origin near the apex with an apical loop of about 0.25 turn before its junction with the girdle. It sweeps posteriorly as a deep trough (fig. OO, 10) for 0.5 turn before joining the girdle distally, beyond which it sweeps around the dorsal face of the hypocone as a deep trough for another 0.5 turn, ending close to the left side of the antapex.

The ocellus is situated less than 0.2 of the total length of the body from the apex on the ventral side at the left of the sulcus. Its axis is in part almost horizontal, but the lens is curved posterosinistrally nearly 45°. In Schütt's first figure (fig. OO, 9), drawn from a fresh, living cell, the ocellus is figured, and described in his explanation of plates, as having a club-shaped, black melanosome with a highly refractive sphere closely connected with it. Several black-pigment masses are present near the border of the girdle and sulcus. In his second figure of the moribund cell (fig. OO, 10) the melanosome is amoeboid and detached pigment masses are more numerous. The lens is apparently disintegrating into spherules, the five rounded bodies close beside the melanosome which he has designated as lens (*Ls*), describing them as highly refractive spherules with a surrounding wall "Y-oil with plastid." These are possibly oil globules, and not the lens divided up into smaller moieties as he has designated them. The presence of oil globules near the ocellus is a phenomenon of very frequent occurrence throughout the whole genus. On the other hand, the whole evidence throughout the group points toward

the stability of the lens as an organ of definite outline and shape which does not break up into smaller moieties except in late stages of actual cytolysis.

The nucleus is large, broadly ellipsoidal, situated just posterior to the ocellus and extending nearly to the antapex. Moniliform chromatin threads are plainly evident. Its major and minor axes are 0.6 and 0.4 transdiameter in length respectively.

No pusules have been figured by Schütt. The protoplasm is finely granular with a marginal zone which apparently covers most of the body, and consists of rodlets which are placed at right angles to the surface. In cross-section these appear as circular in outline with a definite border and central mass. In preparation fixed in osmic acid these rodlets are replaced by elongated vacuoles which in a surface view appear as irregular openings, or a network, with meshes of varying sizes, and all apparently much larger than the circles in the optical section from the living specimen.

Scattered through the protoplasm are a number of rosy globules of varying sizes which he designates as oil masses. These change their size easily, giving off part of their substance in smaller droplets. Near the ocellus is a large, yellowish food mass. The coloring of the body is evidently confined to the red oil globules, the protoplasm being left colorless, with no mention made of it in his explanations.

DIMENSIONS.—Length, 91$\mu$; transdiameter, 80$\mu$; major and minor axes of the nucleus, 49$\mu$ and 35$\mu$ respectively; longest diameter of the ocellus, 30$\mu$.

OCCURRENCE.—Figured by Schütt (1895) in his Plankton Expedition monograph, presumably from the Atlantic or Bay of Naples.

COMPARISONS.—*Pouchetia compacta* has the ocellus farther anterior than any other species in the genus. In fact, it is located in the most anterior part of the hypocone, immediately adjacent to the region of the anterior flagellar pore. The nearest approach to it in this feature is found in *P. polyphemus* (Pouchet), as oriented by us. The ocellus is clearly of the integrated type. The extensive antapical loop of the sulcus beyond the probable location of the posterior flagellar pore is not unlike that found in other large species, such as *P. violescens* and *P. juno*.

In view of the fact that in *Pouchetia* generally (see text figs. OO and PP) the nucleus lies anterior to the ocellus it is more than probable that Schütt's orientation (1895) is reversed and that the ocellus is posterior in *P. compacta*, as it is in other species. We leave the orientation, however, as Schütt delineates it, until the species is rediscovered when the orientation can be accurately determined.

SYNONYMY.—This species was figured by Schütt (1895, pl. 27, fig. $97_{1-7}$) and named *Pouchetia contorta* in his accompanying explanation of plates (pp. 169, 170). In text references (pp. 96, 97) he cites two of these figures (fig. $97_{1-2}$) as *P. compacta*, and on an earlier page (p. 85) cites the figures without quoting the name of the species figured. The question might arise which is the valid name under these circumstances. The name *compacta* on pages 96–97 has priority by position over *contorta*, on pages 169–170, unless it be held that the prior citation, on page 85 of the figures without name, carries with it the explanation of the figures on pages 169–170 with the name *contorta* assigned thereon to the figures cited. It seems best to apply the law of priority by position literally and to give *compacta* precedence over *contorta*.

### **Pouchetia fusus** Schütt

Text figure PP, 1

*Pouchetia fusus* Schütt (1895), p. 96, pl. 26, fig. 94; (1896), p. 6, fig. 8.
*P. fusus,* Delage et Hèrouard (1896), p. 384, fig. 668.
*P. fusus,* Lemmermann (1899), p. 360.
*P. fusus,* Cavers (1913), pp. 182, 183, fig. $9_{17}$.
*P. fusus,* Lühe (1913), p. 230, fig. 230, ocellus lacking.
*P. fusus,* Lebour (1917*b*), p. 198.

DIAGNOSIS.—A medium sized species with fusiform body, its length 2.33 transdiameters; girdle a descending left spiral of 2 turns, displaced 1.33 transdiameters; sulcus with 1 turn, without anterior and posterior loops; ocellus premedian with bipolar lens and circular equatorial pigment mass. Length, 94$\mu$. Bay of Naples or Atlantic (?); Plymouth Sound, England, September.

DESCRIPTION.—The body is stout fusiform, widest at the middle, more tapering posteriorly, its length 2.33 transdiameters at the widest part. The epicone has a length at its left and right sides of about 0.20 and 0.75 respectively of the total length of the body. It is thus a trifle shorter than the hypocone, but being stouter anteriorly has about the same volume as the longer hypocone. The anterior part is convex conical (55°) with rounded apex. The hypocone is more tapering (50°), less rounded at the antapex and somewhat less symmetrical. The dorsoventral and transverse diameters are equal.

The girdle begins at the anterior flagellar pore, located at its junction with the sulcus, about 0.2 total length of the body from the apex, forms a descending left spiral of almost two full regular turns, with a total displacement of 1.33 transdiameters or 0.56 total length. The furrow is deeply impressed and has a width of 0.14 transdiameter. The sulcus begins a short distance below the apex of the epicone, runs posteriorly to the junction with the girdle, and turns in a descending left spiral for nearly a full turn to its posterior junction with the girdle, beyond which it runs posteriorly nearly to the antapex in the median plane. There is thus neither an anterior nor a posterior loop, and there is no sulcal notch at the antapex. Both flagellar pores are near the midventral line. The transverse flagellum makes more than one turn and the longitudinal exceeds 0.5 of the length of the body.

The ocellus is peculiar in two respects: its location is deep in the cytoplasm almost in the axis of the body anterior to the middle and to the greatest diameter, and it is bipolar. Its length is about 0.65 transdiameter and its axis is almost parallel to, or coincident with, the axis of the body (without torsion). The narrow intervals between the turns of the girdle and sulcus do not permit so large a lens to occupy the usual peripheral position at the immediate left of the sulcus. It thus appears to be forced into the interior by the torsion of the narrow body. It consists of a bipolar lens with an encircling equatorial pigment mass. The exposed ends are spheroidal, about 0.3 transdiameter in diameter, of equal size, with about 0.25 diameter covered by the pigment mass. This is a ringlike structure, the diameter of which is 1.2 and the length about 0.6 of that of a lens. It is black with a reddish brown center. Lebour (1917*b*) says it is dark red and was seen breaking up into small red spots in one case. Except for a small globule of black pigment on the posterior lip of the girdle on the dorsal side no other structures are noted by Schütt (1895).

DIMENSIONS.—Length, 94$\mu$; transdiameter, 41$\mu$; length of ocellus, 27$\mu$.

OCCURRENCE.—Figured by Schütt (1895) from the collections of the Plankton Expedition, presumably from the Bay of Naples or the Atlantic. The only other record is that of Miss Lebour (1917*b*), who reports it as rare in September in the plankton from Plymouth Sound, England.

Comparisons.—This species is unique in *Pouchetia* and in the whole family Pouchetiidae in the structure of the ocellus. In shape of body it is near *Nematodinium torpedo.* The straight course of the sulcus on epicone and hypocone above and below the girdle is scarcely equaled elsewhere in *Pouchetia.* It is thus one of the most divergent species in that genus, although it becomes the type species of the genus (by specification) and is the only one cited by Schütt (1896) when he characterized *Pouchetia.* Because of the compound lens we place it in the subgenus *Pouchetia.*

## **Pouchetia juno** Schütt

Text figure OO, 3

*Pouchetia juno* Schütt (1895), pp. 6, 87, 97, 170, pl. 27, figs. $98_{1-2}$, $99_{1-2}$.
*P. juno,* Lemmermann (1899), p. 360.
*P. juno,* Lang (1901), p. 161, fig. 175*b*.
*P. nigra,* Pavillard (1905), in part, p. 47, as a synonym (?) of *P. nigra* (Pouchet) Lemmermann (= *Protopsis nigra* (Pouchet) Kofoid and Swezy).
*P. juno,* Lühe (1913), p. 320, fig. 322 B.

Diagnosis.—A large species, body stout fusiform, constricted, its length 2 transdiameters; girdle a descending left spiral of 1.5 turns; sulcus with torsion of 2.5 turns, with apical loop of 1.25 turns; ocellus concentrated, median, horizontal; lens spheroidal; melanosome massive. Length, 141μ. Atlantic, Pacific off La Jolla, California, July.

Description.—The body is stout fusiform, its length 2–2.3 transdiameters measured at the widest point which is about equatorial, deeply constricted by the sulcus, and concave in outline in the central section when fully elongated (Schütt, 1895, pl. 27, fig. $99_2$). The epicone is 0.4 of its own length longer than the hypocone. Its length at the proximal and distal ends of the girdle is 0.30–0.43 and about 0.84 respectively of the total length of the body. It is rounded subconical at an angle of about 40°–50°, and the apex is flat or rounded and evidently much modified by the terminal sulcus. The hypocone has a length at the two ends of the girdle of 0.57–0.70 and 0.11 respectively of the total length of the body, and is more broadly subconical (55°) with a truncate antapex notched by the distal end of the sulcus.

The girdle forms a uniformly descending left spiral, 20°–25° from the horizontal. It joins the sulcus anteriorly at 0.30–0.43 total length from the anterior end and reunites with it distally at about 0.11 of the total length from the postmargin, on the opposite side of the body from its origin. It thus makes 1.5 turns and is displaced about 0.45–0.60 total length. The furrow is 0.1 transdiameter in width and is very deeply sunken into the plasma, with prominent overhanging anterior lip.

The sulcus runs from apex to antapex and has a total torsion of about 2.5 turns. Schütt's two figures are irreconcilable as to the course of this structure. His first figure (1895, pl. 27, fig. $98_1$) more correctly portrays the course and in our text figure (fig. OO, 3) we have reproduced his second figure modified to bring out the correct interpretation, especially with reference to the posterior end of the sulcus. The long channel (?) seen in the posterior part from which the posterior flagellum seems to emerge may really have been the posterior pusule opening posteriorly at the posterior flagellar pore and not the sulcus seen through the body from above. We so interpret it in our modified figure. The sulcus has an apical loop of 1–1.5 turns which may surround a small apical eminence. The intercingular section makes about 1.2 turns crossing

the protuberant ocellus, flattening the spiral distally to 20° from the horizontal and turning abruptly posteriorly at the posterior junction. The anterior flagellar pore is at the anterior junction, and the posterior pore immediately at the posteroir junction of girdle and sulcus.

The ocellus is slightly postmedian in location, at the left of the anterior part of the intercingular sulcus. Its length is 0.5 transdiameter and the lens is directed horizontally to the left side of the body, on whose margin about 0.5 of the body of the lens protrudes. The ocellus consists of a spheroidal lens about the same size as the melanosome and 0.33 transdiameter across. It is hyaline, finely laminate and has a narrow peripheral layer strongly differentiated. In encysted and moribund animals it becomes more ovoidal in form, with the larger end protruding and the melanosome sends out short stout processes. In the normal condition the black melanosome is a hemispheroidal or rounded mass in which one face of the lens is lightly imbedded. No bright colored central core was noted. Small detached strands of brownish-black melanin lie parallel to the girdle in its margins.

The nucleus is ellipsoidal, located anteriorly, and has about twenty beaded spiral chromatin strands across one face. Its major and minor axes are 0.9 and 0.7 transdiameter in length respectively. One or more long clavate pusules open anteriorly at the anterior flagellar pore and what appears to be a long slender one passing anteriorly to the ocellus opens posteriorly at the posterior pore. Irregular rounded double-contoured platysomes fill the peripheral plasma, showing locally slight indications of linear arrangement. There are also the faintest of suggestions of linear striae in the pellicle which persists on plasmolysis (Schütt, 1895).

The color of this organism is neither figured nor stated by Schütt. Our own observations are restricted to a single individual recorded at the time in our notes as having dark purplish black granules along the girdle as cytolysis approached.

DIMENSIONS.—Length, 125$\mu$; transdiameter, 70$\mu$; length of ocellus, 21$\mu$; of nucleus, 32$\mu$ and 22$\mu$.

OCCURRENCE.—One individual was taken July 3, 1906, 2.75 miles of La Jolla, California, in a haul of a No. 20 net from 155 meters to the surface in a surface temperature of 20°5 C.

Schütt (1895) figures this species, presumably from the Bay of Naples or from the collections of the Plankton Expedition in the Atlantic.

COMPARISONS.—*Pouchetia juno* is one of the most highly specialized species of the subgenus *Pouchetiella* with integrated ocellus. Its specialization is indicated in the spherical, laminate lens, compact melanosome, median location, and horizontal position of the ocellus; also by the extreme torsion of the sulcus of 2.5 turns, its extent from apex to antapex, and the prolonged apical loop.

It is closely related to *P. violescens,* having the same type of ocellus, similarly located, the same long apical loop, and about the same torsion of sulcus. It differs, apparently, in coloration, proportions of body, and in the course of the apical loop, relative size of lens and melanosome, and striations. *P. juno* has not been reported to be violet in color, is more fusiform, does not have the apical loop crossing the apex, but encircling it only, has the lens much larger than the pigment mass instead of equal to it, and has exceedingly faint striations instead of prominent ones. The possibility of both falling within the range of one variable species is not excluded. More material is needed to determine this with certainty.

SYNONYMY.—Pavillard (1905, p. 47) cites it tentatively as a synonym of *Pouchetia nigra* (Pouchet) Lemmermann (1899). This allocation seems to us untenable since the course of the girdle and sulcus in the two species is wholly different. Moreover, the ocellus of *Protopsis nigra* (Pouchet) Kofoid and Swezy is of the diffuse type, while that of *P. juno* is an integrated one and highly specialized. In addition *Protopsis nigra* is a small species, length 74µ, while *Pouchetia juno* is a large one, 125–141µ in length.

## **Pouchetia maculata** sp. nov.

Plate 11, figure 119; text figures T, 2; PP, 12; QQ, 1

DIAGNOSIS.—A small species, ovoidal, wider anteriorly, length 1.3 transdiameters; girdle a descending left spiral of 1.5 circumference; ocellus postmedian, horizontal, with segmented elongated lens and a black melanosome with a lighter central core. Length, 53µ to 58µ. Pacific off La Jolla, California, July.

DESCRIPTION.—The body is ovoidal, somewhat flattened laterally and contracting posteriorly, irregular in outline owing to the projecting lobes between furrows on the ventral face. Its widest diameter is found some distance above the middle of the body plane. The epicone and hypocone are subequal. The epicone is very broadly rounded, having a length above the anterior pore of 0.3 and from its posterior extremity of 0.8 of the total body length. The apex is flaring hemispherical. The hypocone is very deeply cleft on the ventral side of the sulcus, the intervening ridges of which may be more or less pronounced. The antapex is broadly rounded and not cleft by the sulcal notch. There is an antapical process, more or less pushed anteroventrally, which lies at the right of the longitudinal flagellum. It is variable in form in different aspects and differs in the two individuals under observation. It is probably somewhat mobile and may represent the first step in the evolution of the tentacle as developed in *Erythropsis*. In one of our specimens (pl. 11, fig. 119) it is a short rounded lobe projecting posteroventrally near the ocellus at the right of the flagellum. Its diameter in an obliquely lateral view is a little more than its length, which is 0.14 transdiameter. Its dorsoventral extension is thus not great (fig. QQ, 2). On the other hand, this antapical process is more posterior in location, and has a much greater extension as a long ridge or crest more than twice as long as it is wide or high. It terminates abruptly on the dorsal and median faces. It is possible that there is a posterior loop of the sulcus around this process.

The girdle joins the sulcus anteriorly at a point 0.3 and posteriorly 0.8 of the total length of the body from the apex. It passes in a semicircle around the body before the descending left spiral steepens sharply in its distal quadrant. It makes 1.5 turns before meeting the sulcus distally at a point about 0.2 of the total length of the body from the antapex. The total displacement is 0.5 total length of body or 0.68 transdiameter. For most of its extent it is deeply embedded, the proximal border forming an overhanging ridge. On the ventral side this becomes more pronounced and is shown on both borders. The anterior flagellar pore is located at its anterior and the posterior pore at its posterior junction with the sulcus. The transverse flagellum traverses 0.3 of its total length. The longitudinal flagellum equals or exceeds the length of the body in length.

The sulcus forms a slight loop around the right face of the epicone, taking its origin at the left of the apex. It descends posteriorly, sweeping around nearly 0.5 of a turn before meeting the girdle distally, beyond which it turns to the right as a very deep groove, the proximal border

of which forms a deeply overhanging lip. It is a shallow channel on the epicone, but becomes more deeply embedded as it proceeds posteriorly. This, with the deeply embedded girdle, breaks up the ventral face into three more or less projecting lips, the lower one of which may show a greater protrusion.

The ocellus is large, about 0.4 transdiameter in length, located some distance below the equatorial plane to the left of the sulcus. Its axis is horizontal and it is directed ventrally. The lens is oblong in shape and is composed of four moieties closely joined together, of a clear hyaline material and greenish in color, closely embedding its base in the large rotund, black, amoeboid melanosome with its lighter central core. The ocellus is of the concentrated or simple type, although the lamination of the lens still shows its origin from separate parts (pl. 11, fig. 119). In two other individuals the lens (fig. QQ) was less elongated and less distinctly segmented.

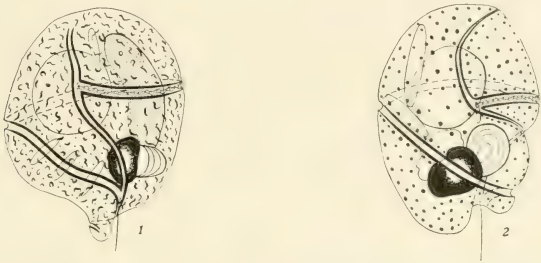


Fig. QQ. *Pouchetia maculata* sp. nov. Two individuals showing variations in size and shape of lens and in pigmentation. × 710.

The nucleus in both individuals figured has the elongated, enlarged, somewhat reniform contour characteristic of predivision stages. Its major and minor axes are 0.6 and 0.4 transdiameter respectively. Fine beaded parallel chromatin strands follow its major axis. In what is apparently the usual vegetative condition its major and minor axes are about 0.5 and 0.3 transdiameter respectively.

A small pink club-shaped pusule opens into the anterior flagellar pore. None was noted at the posterior pore. The cytoplasm is clear and granular, but so filled with colored masses as to give the whole body a dense appearance. In the half of the organism are a number, varying from 2 to 6, of long, slender, green rodlets. These are generally placed at right angles to the surface and point toward the center of the body. In the posterior region of the individual figured in color (pl. 11, fig. 119) was located a large, rounded, reddish-brown food mass, and many very small green rodlets apparently differing in no way except in size from the larger ones. These radial structures appear to be accumulations of substances along paths in which substances in metabolism are in transit. Small green oil droplets are abundant near the surface. The peripheral layer also contains, abundantly scattered over the entire surface, irregular or spheroidal pigment masses of sooty black color. In one individual observed the peripheral plasma was strewn with this pigment in the form of fine black rods, curved commas, S- and U-shaped figures, and irregular short curves as well as in small grains. While under observation these began to round up in spherules prior to cytolysis. The general color of the organism is a bluish grey with a reddish-brownish tinge in one case in the posterior region, evidently due to the solution of the adjacent food mass.

DIMENSIONS.—Length, 53–58$\mu$; transdiameter, 37–44$\mu$; axes of nucleus, 19–35$\mu$ and 10–18$\mu$.

OCCURRENCE.—Two individuals were taken July 26, 1917, 2.5 miles off La Jolla, California, with a No. 25 silk net in a haul from 80 meters to the surface and in a surface temperature of 21°4 C. On July 23 another individual was taken at approximately the same place and with the same apparatus, the surface temperature being 20°2 C.

ACTIVITIES.—One individual seen was still active and circled feebly on the substrate in narrow, anticlockwise spirals with spasmodic jerks, due probably to intermittent adhesions of the flagellar apparatus.

COMPARISONS.—This species is a generalized member of the subgenus *Pouchetiella*, which has a concentrated or integrated ocellus. In the posterior location of the ocellus, its horizontal axis, and the presence of an antapical lobe or process, it is like *Proterythropsis crassicaudata* and also possesses in common with it distributed peripheral granules of pigment. In the latter species, however, the pigment is red instead of black and is less abundant with more of a linear distribution, the lens is more distinctly lobed, and the antapical process much longer. The linear form of the distributed peripheral pigment is almost identical with that in *Protopsis nigra* (Pouchet, 1887, pl. 10, fig. 2).

## **Pouchetia maxima** sp. nov.

Plate 6, figure 61; text figure OO, 2

DIAGNOSIS.—Large species, ellipsoidal, its length 1.4 transdiameters; girdle forms a descending left spiral of 1.5 turns, displacement 0.72 total length; torsion 0.75 turn, ocellus concentrated, median, horizontal; lens hemispherical, melanosome with reddish brown central core; plasma pale lavender. Length, 145$\mu$. Pacific off La Jolla, California, July.

DESCRIPTION.—The body is subellipsoidal with the dorsal side more convex, and the ventral flattened. Its length is 1.4 transdiameters at the widest part of the body which is equatorial. The epicone is shorter than the hypocone by 0.12 the length of the former, is asymmetrically hemispherical at the apex, being tilted to the left and ventrally, and has a length above the anterior pore of 0.06 and at its distal termination of 0.80 of the total length of the body. The hypocone has a length at the proximal and distal ends of the girdle of 0.94 and 0.20 respectively of the total length of the body. It is somewhat wider and more voluminous than the epicone. The antapex is broadly rounded and slightly asymmetrical, the sulcus terminating in a trough on the side of the body opposite to that of the anterior pore but without a terminal sulcal notch.

The broad girdle joins the sulcus anteriorly at a point 0.06 of the total length of the body from the apex. It immediately curves posteriorly at about 40° from the horizontal for 0.5 turn before crossing the dorsal side almost horizontally, then again turns posteriorly at about 45° for 0.5 turn, slackening in the distal 0.25 turn almost to the horizontal again, making in all 1.5 turns before joining the sulcus distally, at a point 0.2 of the total length of the body from the antapex. Its total displacement is thus about 0.75 length of the body. The anterior flagellar pore lies at the anterior junction of the girdle and sulcus, the posterior one posterior to the distal junction. The furrow has a width of 0.09 transdiameter and is not deeply impressed. The transverse flagellum traverses the girdle for about 0.25 of its length. The pores open on opposite faces of the body.

The sulcus takes origin in a rounded depression only slightly above the anterior flagellar pore. It sweeps around the body as a narrow shallow trough about 0.33 the width of the girdle for 0.75 of its circumference, ending on the right margin of the dorsal side of the antapex. The sulcus widens to three times its width above, after its posterior junction with the girdle.

The ocellus is situated on the ventral face at the left of the sulcus, slightly anterior to the equator. Its length is about 0.25 transdiameter and its axis horizontal. It is directed to the left. It consists of a hemispherical melanosome with a rufous central core in which the base of the smaller lens is embedded. Near the lens is a horizontal row of five unequal, highly refractive spherules appressed in one mass, the one nearest the lens being a nearly spherical hyaline mass. They are composed of greenish opaque material resembling the lens in color but less hyaline. They appear to be products of metabolism rather than parts of a lens of the diffuse type. Several masses of rufous-black pigment are scattered along the anterior border of the girdle below the ocellus.

The nucleus is large, spheroidal, ovoidal or ellipsoidal, and centrally located. Distinct chromatin strands follow its major axis. Its major and minor axes are 0.7–0.9 and 0.6–0.4 transdiameter in length respectively.

A small ovoidal pusule opens anteriorly into the anterior flagellar pore. The cytoplasm is finely granular with few to many food vacuoles. In the individual figured the irregular wrinkled skirt of protoplasm protruding from the antapex is the discharge vent opened by the ejection of a large food mass. The same appearance has been noted in other forms with the actual discharge of a food mass. Later it was completely retracted in the individual figured.

The surface of the body presents a number of distinct longitudinal striations on the hypocone, sixteen on one face. There are faint indications of striae on the central section of the epicone, but none elsewhere. There are no peripheral vacuoles other than slight accumulations along the striae.

The color is a pale lavender diffused through the cytoplasm, being more dense at the periphery than throughout the main body and a trifle darker anteriorly, suggesting an axial gradient in metabolism.

DIMENSIONS.—Length, 145$\mu$; transdiameter, 92$\mu$; axes of nucleus, 60$\mu$ and 63$\mu$; length of ocellus, 20$\mu$.

OCCURRENCE.—One individual was taken in a haul made 4 miles off La Jolla, California, on July 11, 1917, with a No. 25 silk net from 80 meters to the surface and in a surface temperature of 19°7 C.

ACTIVITIES.—The turns of the spiral of the contracted transverse flagellum were very close set and the waves of contraction running through it distally were extraordinarily rapid. The animal moved intermittently in clockwise circles of a diameter several times its length, without rotation on its axis. The progress was noticeably intermittent and jerking and is due either to the temporary attachment of the trailing flagellum to the substrate or to its intermittent action, apparently to the latter primarily.

COMPARISONS.—This is a very highly specialized representative of the subgenus *Pouchetia* with integrated ocellus. Both lens and melanosome are compact and their union is intimate. In volume also it is a large species, in fact the largest in the genus. It shares the structural features of median ocellus of integrated type in a horizontal position and large size of body with *P. juno* (fig. OO, 3) and *P. violescens* (fig. OO, 1). It differs from them in one important feature, namely, the very great displacement between the proximal and

distal ends of the girdle, 0.75 length of body, as compared with 0.5 or less in the two species named. The consequence is that the apical loop of the sulcus, so prominent in these two species, is practically eliminated in *P. maxima*. It is also striated as are *P. violescens* and *P. striata* (figs. OO, 1, 8), thus adding development of surface markings and marked expansion of the furrow and sulcus to the other indications of specialization.

## **Pouchetia panamensis** Kofoid

Text figure PP, 7

*Pouchetia panamensis* Kofoid (1907*b*), pp. 164, 167, pl. 1, fig. 7.

Diagnosis.—A minute species with ovoidal body, its length 1.6 transdiameters; girdle a descending left spiral, displaced nearly 0.7 transdiameter, and making 1.25 turns; sulcus extends nearly to apex, its torsion nearly 0.5 turn; ocellus subspheroidal with minute central lens; plasma rose pink. Length, 34μ. Pacific, Bay of Panama, October.

Description.—The body is slightly ovoidal, widest below the equator, its length 1.6 greatest transdiameters. The epicone and hypocone are almost equal, apex hemispherical, antapex more pointed, hypocone somewhat flattened ventrally. The girdle forms a descending right spiral with a very regular descent for 1.25 turns and has total vertical displacement of about 0.7 transdiameter, or 0.43 the total length. The furrow is slightly impressed without marked lips and is relatively very wide, being 0.16 transdiameter in width. The sulcus is about 0.25 the width of the girdle and extends from within 0.12 of the total length of the body from the apex to the posterior end, where it flares out in a terminal pocket. The total torsion of the sulcus to the left is a little less than 0.5 turn. The flagellar pores are at the junctions with the girdle. The anterior flagellum runs the entire length of the girdle; the length of the longitudinal one is about 0.5 the length of the body.

The ocellus lies at the left of the junction of the sulcus and the distal end of the girdle. It is a minute body about 0.2 transdiameter in diameter. It consists of a subspheroidal, notched, black melanosome with irregular surface in the left anterior side, of which a very small spherical lens is deeply embedded, so that the melanosome forms a stout crescent about it. The lens as exposed is only about 0.25 the diameter of the melanosome in diameter. The nucleus is also relatively small. It is an ellipsoidal body centrally located below the equator with its major and minor axes respectively 0.40 and 0.24 transdiameter in length. It lies obliquely to the main axis. Spherical droplets are scattered in the peripheral plasma. The color is a diffuse rose pink fading out posteriorly and deepest near the anterior end.

One individual was enclosed in a concentric, trilamellate cyst, the length of which was nearly three times the length of the body. Its surface was gelatinous and was covered with adherent particles of débris.

Dimensions.—Length, 34μ; transdiameter, 21μ; ocellus, 4μ; nucleus, 8μ.

Occurrence.—Several individuals seen in surface collections of plankton made with a No. 20 silk net by the senior author while on the Agassiz Expedition to the Eastern Tropical Pacific in 1904–05 in the Bay of Panama, at the ship's anchorage, October 23, 1904, in a surface temperature of about 27° C.

Comparisons.—With the exception of *P. parva* Lohmann, *P. panamensis* is the smallest species in the genus. It has the lens reduced to the merest

rudiment. It is one of the simplest species of the subgenus *Pouchetiella* with ocellus of the concentrated or integrated type and has no nearly related species in so far as proportions, furrows, and ocellus reveal relationships.

### Pouchetia parva Lohmann

Text figure PP, 6

*Pouchetia parva* Lohmann (1908), pp. 147, 202, 252, 264, 366, table B, pl. 17, fig. 23. Figure inverted.

*P. paron,* Lohmann (1908), p. 369. *Lapsus.*

*P. parva,* Paulsen (1908), p. 106, fig. 148. Figure inverted.

*P. parva,* Lohmann (1911), pp. 30, 31, pl. 1, fig. 5; pl. 4, fig. 12*d*.

*P. parva,* Ostenfeld (1913), p. 338.

*P. parva,* Lebour (1917*b*), p. 198.

DIAGNOSIS.—A minute species, irregularly and asymmetrically ovoidal, its length 1.6 transdiameters; girdle making probably 1.5 turns with considerable displacement; sulcus unknown; ocellus postmedian, lens spheroidal irregularly laminate, melanosome pyriform in outline; color, ochraceous. Length, 33$\mu$. Baltic at Kiel; Plymouth Sound.

DESCRIPTION.—Lohmann's (1908, 1911) figures of this small species are so incomplete as to make even its generic allocation a matter of uncertainty, especially since the girdle and sulcus are not shown. The following account is based on his figure interpreted in the light of our comparative knowledge of the genus.

The body is irregularly ovoidal and asymmetrical, or even almost biconical in its contour, with the shorter cone or broader end anterior. Both Lohmann (1908, 1911) and Paulsen (1908) invert the figure and place the pointed end anterior. However, the relations of the ocellus are in harmony with those elsewhere in the genus if we invert Lohmann's figure, place the pointed end posterior and thus point the lens anterosinistrally. The indications of the girdle also favor such an interpretation. The length is 1.6 transdiameters at the widest part which is anterior to the girdle and to the middle. The epicone appears to exceed the hypocone in size. The epicone is convex subconical with an angle of about 50° and a broadly rounded apex. The hypocone has about the same angle, is less symmetrical, more prolonged, protuberant near the ocellus, excavated below it, and terminates in contracted, bluntly pointed antapex, reflexed to the right and dorsally.

The absence of the ochraceous color in this antapical tip in Lohmann's (1911, pl. 4, fig. 12*d*) third figure of this species appears to be an oversight. Otherwise one might interpret it as a developing cyst detached only posteriorly from the surface pellicle of the body. In his second figure (1911, pl. 1, fig. 5), drawn without a cyst wall, there is no suggestion that this extension is not a part of the body, and in the original figure (pl. 17, fig. 23) it is colored with the same ochraceous tint as the remainder of the body.

The girdle is not portrayed sufficiently to enable one to define its course with certainty. It forms a descending left spiral. The asymmetrical antapex is suggestive of at least 1.5 turns and a displacement of about 0.75 transdiameter. The furrow, as drawn, is only slightly impressed. The sulcus is not indicated in any way, unless it be that the line across the antapex represents a posterior turn of this groove somewhat as in *Nematodinium*. If this be sulcus there may be at least a full turn of the sulcus about the body.

The ocellus is quite large, 0.5 transdiameter in length, and is located just posterior to the middle of the body, below the girdle, and apparently in the typical position at the left of the intercingular sulcus. Its axis stands at about 45° above the horizontal and it is directed anterosinistrally. It is quite protuberant and appears to be crowded against the sulcus. It is of the simple or concentrated type, consisting of a spherical lens and massive pyriform (?) melanosome. The lens is somewhat irregularly subdivided into several unequal lamellae and is slightly embedded on one face in the larger end of the melanosome, which is larger than the lens, its major and minor axes being respectively 1.5 and 1.25 diameters of the lens in length.

The color of the body is diffuse ochraceous. This species is often found in a transparent, close fitting cyst within which binary fission occurs with resulting temporary chain formation of the two sister organisms.

DIMENSIONS.—Length, 33$\mu$; greatest transdiameter, 20$\mu$; length of the ocellus, 10$\mu$.

OCCURRENCE.—Reported by Lohmann (1908, 1911) from the plankton of the Baltic Sea at the entrance to Kiel Harbor from April to November, in surface temperatures of 5° C to 19° C. The plankton was collected by the centrifuge method and the numbers per 100 liters range from less than 500 or too few for enumeration to 50,000. This maximum was found on May 16, 1906, at the surface in a temperature of 12·6 C, as shown in Lohmann's table B. His statement in the text (1908, p. 263) that the maximum was 230,000 appears to be in contradiction to the table and to his own previous citation of the 50,000 maximum. He finds the species avoiding the deeper waters at his collecting station, where the depth was 15 to 16 meters. On the 23 days on which it was found in the series of 60 sets of samples from different levels from April 12, 1905, to August 17, 1906, it occurred 15 times at the surface, 12 times at 5 meters, and only 3 times at 15 meters. The influence of light is thus evident in its distribution.

Miss Lebour (1917*b*) reports it from Plymouth Sound as "frequent in summer, especially in June." She states, however, that "this species is very like Pouchet's figure (1885) of *P. polyphemus* var. *nigra*. The pigment, however, in his species is red and this is always black." Since Pouchet did not describe his *Gymnodinium polyphemus* var. *nigrum* until 1887, and never stated, so far as we can find, that its pigment was red, it seems that Miss Lebour must consider his var. *nigrum* (1887) as the equivalent of his *polyphemus* (1885), although his figures of 1887 show black pigment, but no red. As shown elsewhere by us (p. 000), we regard Pouchet's *G. polyphemus* (1885) and his *G. polyphemus* vars. *nigrum* and *roseum* (1887) as three distinct species. The uncertainty thus raised by Miss Lebour's statement makes the allocation of her record of occurrence to *P. parva* Lohmann somewhat tentative.

COMPARISONS.—This is the smallest species known in the genus *Pouchetia*. It is a member of the subgenus *Pouchetiella* with concentrated or simple ocellus, and, in so far as indicated by the structure of the ocellus, is nearest *P. juno*, *P. purpurata*, *P. rubescens*, and *P. violescens*, though probably of simpler organization than these species in other features. There appears to be no probability that it is near *Protopsis nigra* (*Gymnodinium polyphemus* var. *nigrum*

Pouchet), as intimated by Miss Lebour (1917*b*), since the ocellus is of the diffuse type in *Protopsis nigra* and of the simple or concentrated type in *Pouchetia parva.* The shape, size, and proportions of the body are quite different in the two and the girdle, as we have indicated above, appears to be of the *Pouchetia* type with torsion, rather than of the *Gymnodinium* type with none, as in *Protopsis.*

## **Pouchetia polyphemus** (Pouchet) emend.

Text figure OO, 11

"Voisin de *Gymn* [*odinium*] *spirale* Bergh et *Archimedis* Pouch." Pouchet (1885*a*), pp. 38–41. *Pouchetia polyphemus sensu latu.* Indeterminable.

"*Peridinium* voisin de *Gymnodinium spirale,*" Pouchet (1885*a*), p. 85, pl. 2, figs. 1*a-c.* Three different forms figured, all *Pouchetia,* but indeterminable.

*Gymnodinium polyphemus* Pouchet (1885*b*), pp. 529–531, pl. 26, fig. III. Fig. IV is a different and an indeterminate species of *Pouchetia;* (1886), pp. 223–224; (1887), pp. 101, 112; (1894), p. 175.

*Gymnodiniums polyphemus* Pouchet (1885*b*), p. 529. *Lapsus.*

*Gymnodinium polyphemus* Pouchet (1887), pl. 10, bottom, *Lapsus.* Plate contains figures of *Gymnodinium polyphemus* var. *roseum,* pl. 10, fig. 1 (= *Pouchetia roseum* (Pouchet)) and *Gymnodinium polyphemus* var. *nigrum,* pl. 10, figs. 2 A-B, 3, 4 (= *Protopsis nigra* (Pouchet). Figs. 2 C and 5 are indeterminable.

*Gymnodinium polyphemus,* Schütt (1895), pp. 94, 95.

Diagnosis.—A large species with elongated, curved, ellipsoidal body, length 2.2 transdiameters; girdle with about 1.75 turns, displaced about 0.5 total length of body; sulcus with at least 2 turns, with apical and antapical loops; ocellus premedian, simple, with elongated hemispherical lens and somewhat irregular pigment mass, plasma colorless. Length, 104$\mu$. Atlantic, Concarneau, France; Dyrefjord, Iceland, July and August.

Description.—From our current knowledge of this genus, together with the indications of girdle and sulcus in Pouchet's figure, we are able to complete tentatively the structural features sufficiently to obtain a fairly diagnostic account of this species. This interpretation is represented in the modified figure (text fig. OO, 11) based on Pouchet's (1885*b*, pl. 26, fig. 3), in which we have interpreted his partially drawn sulcus and girdle as beneath instead of on the upper side of the figure as he has drawn them. As is frequently the case in Pouchet's plates, this figure has its posterior end uppermost on the plate.

The body is elongated, ellipsoidal, flattened ventrally, broadly convex dorsally, the dorsal side forming an arc with a radius of 1.5 transdiameters. The length is 2.2 transdiameters at the widest part which is a little anterior to the middle. The epicone and hypocone are subequal. The apex is an asymmetrically flattened hemisphere, with the antapex contracted and deeply cleft by the sulcal indentation with pointed prolongations on either side.

The girdle begins at the right and anterior to the ocellus, about 0.5 transdiameter from the apex, makes about 1.75 turns in a uniformly descending left spiral, joining the sulcus again posteriorly somewhere near 0.5 transdiameter from the antapex. There is a total intercingular displacement of a little more than one transdiameter. The figure was evidently made from a moribund individual and the furrow is scarcely impressed, except anteriorly. The sulcus evidently has well defined anterior and posterior loops beyond the intercingular region. The

anterior loop makes nearly 0.75 turn, the intercingular region has about the same amount of torsion, and the posterior loop somewhat more than 0.5 turn, a total torsion of approximately 2.25 turns. Uncertainty attaches to the distal limit of the sulcus anteriorly and to the exact location of the flagellar pores.

The ocellus is of the concentrated or integrated type. It is located at the anterior angle of the hypocone, 0.33 of the total length from the anterior end at the left of the sulcus and just posterior to the girdle. Its length is 0.25 transdiameter. Its axis appears to be parallel to the major axis of the body and is directed anteriorly. It consists of an elongated subhemispherical lens whose exposed length equals its diameter and a ragged disk of pigment (reddish brown on the plate), the diameter of which is twice that of the lens and 0.25 transdiameter of the body. The color of the pigment of the individual figured is not stated in the pertinent text.

The nucleus was so transparent as to have eluded observation. There is a large clavate pusule near the ocellus, evidently attached to the anterior flagellar pore. The cytoplasm is stated to have been transparent, colorless, and coarsely vacuolated. A red pigment fleck lies on the anterior margin of the anterior loop of the sulcus. Free and encysted forms were seen.

Dimensions.—Length, 104$\mu$; transdiameter, 47$\mu$; length of ocellus, 12$\mu$.

Occurrence.—Figured from the Atlantic at Concarneau, France, by Pouchet (1885*b*) and stated by him later (1892, 1894, p. 170) to occur in typical form in the plankton of Dyrefjord, Iceland, in July and August, at 10° C.

Comparisons.—This species is the only one in *Pouchetia* with an ocellus so far anterior except *P. compacta* Schütt, and there is some doubt about the orientation of that species. *P. fusus* Schütt and *P. maxima* sp. nov. have a premedian ocellus, but not so far anterior as in *P. polyphemus*. The bifid antapex, the character of the anterior and posterior loops of the sulcus, and the orientation of the ocellus combine to confirm the correctness of the orientation which we have given to Pouchet's figure. This species is not far from *P. juno* and *P. violescens* in girdle, sulcus, size, form, and structure and location of the ocellus. The differences between them appear to lie in the color and surface differentiations and in the direction of the axis of the ocellus. *P. polyphemus* is colorless and has neither longitudinal markings nor platysomes; the axis of its ocellus is longitudinal, while in the two species named this axis is horizontal. *P. violsecens* is colored and has longitudinal markings and *P. juno* has peculiar platysomes. *Pouchetia polyphemus* belongs in the subgenus *Pouchetiella*.

Synonymy.—This species was originally described by Pouchet (1884, 1885*a*, *b*), apparently from a complex of forms which he did not clearly analyze, and within which he noted (1885*a*) a considerable range in size, color, and structure, which he imperfectly interpreted, and an inconstancy of occurrence of the ocellus. These facts, with our present knowledge of the group, afford conclusive proof that he confused species of *Pouchetia* with those of other genera, and establish also the probability of confusion of species within the genus of *Pouchetia* itself.

His statement (1886) that the ocellus develops by the fusion of the refringent spherules into one body and the retraction of the pigment into one cap-shaped mass seems rather to be a hypothetical interpretation based on different

individuals or species than an analysis of development. Any delimitation of *P. polyphemus* (Pouchet) must therefore be based upon his figures and such parts of his text as are descriptive thereof.

In his earlier papers (1884, 1885*a*) Pouchet discussed the ocellus and (1885*a*, pl. 2, figs. 1*a-c*) figured several forms, each with an ocellus, but did not designate the species beyond stating in his explanation of the plate that one of them was "voisin de *Gymnodinium spirale*." The two or three forms figured in this paper are, in the absence of comparable material, clearly indeterminable beyond the probability that they belong to the genus *Pouchetia*. It is possible that his figure of the lens will permit the detection of one of these forms when rediscovered.

In a later paper (1885*b*) Pouchet figures, briefly describes, and names *Gymnodinium polyphemus*, a different form from that previously (1885*a*) figured, and at the close of his statement refers the reader to his earlier paper (1885*a*). In view of this sequence we restrict the name *polyphemus* to the organism named in his later paper, delineated in the first of his figures (1885*b*, pl. 26, fig. 3). The second figure (see his pl. 26, fig. 4) is a smaller organism, also with ocellus, in binary fission in a cyst, and so lacking in details as to be wholly indeterminable. It is therefore excluded from *Pouchetia polyphemus*.

Neither Schütt (1895), who established *Pouchetia* and refers to this species, nor Lemmermann (1899), who compiled its species, refer *Gymnodinium polyphemus* to *Pouchetia*. Pouchet's confusion of species might invalidate the accuracy of his record of this same species in the warm waters off the coast of France and in the colder waters off Iceland.

## **Pouchetia poucheti** sp. nov.

Plate 11, figure 125; text figure PP, 4

Diagnosis.—A rather large species; body broadly ellipsoidal, length 1.3 transdiameters; girdle a descending left spiral of 1.2 turns, displaced 0.6 transdiameters: sulcus with apical and antapical loops, torsion 0.75 turn; ocellus diffuse, median, with distributed lens, lobed melanosome, scattered pigment; color, bluish green. Length, 73μ. Pacific off La Jolla, July.

Description.—Body rotund, broadly ellipsoidal with slight irregularities. The epicone is nearly 0.25 smaller in length than the hypocone. Its apex is broadly rounded, higher at the right end, its outline notched on the right side by the apical loop of the sulcus, which here reaches the apex. It has a length above the anterior flagellar pore of 0.3 and at the distal extremity of the girdle of 0.8 of the total length of the body. The hypocone is also broadly but asymmetrically rounded, being prolonged beyond the hemispherical and slightly pointed at the right with its outline somewhat irregular on the left due to the shallow trough made by the antapical section of the sulcus. The shallow sulcal notch lies 0.3 transdiameter to the left of the antapex.

The anterior junction of the girdle and sulcus is located 0.3 of the total length of the body from the apex. The girdle passes around the body in a descending left spiral which in the proximal 0.5 turn is nearly horizontal and is then deflected to a uniform slope of 25° from the

horizontal for the rest of its course. It meets the sulcus at a point 0.16 of the length of the body from the antapex. It forms a broad trough in a shallow constriction with the borders slightly overhanging. The anterior flagellar pore is located at the anterior junction of the girdle and sulcus and the posterior pore is found at the postmargin beyond the posterior junction of girdle and sulcus about the width of a girdle. The transverse flagellum traverses about 0.2 of the length of the girdle.

The sulcus invades the hypocone in a broad apical loop of 0.5 turn, terminating near the apex. It forms a broad channel, only slightly narrower than the girdle, the lips on the epicone forming a high ridge on its left and a lesser one on its right side. In its course below the anterior flagellar pore it forms a deep trough which becomes shallower on reaching its distal junction with the girdle, and continues so in its path down the hypocone to its termination to the left of the antapex. It forms an irregular descending left spiral with torsion of 0.75 turn. It is not improbable that an antapical loop completes a full turn dorsally.

The ocellus is situated in the equatorial region, at the left of the intercingular sulcus. It is of the diffuse type in its least integrated stage. It consists of a loosely aggregated group of lenses and scattered melanosome. The lens is formed of six spherical, clear, bluish hyaline bodies loosely massed together in an irregular linear series 0.33 transdiameter in length. The melanosome is composed of more than a score of irregular, unequal spheroids of black pigment, varying in size from 0.5–6$\mu$ in diameter and scattered in the peripheral plasma at the left and posterior to the lenses, from the left of the anterior flagellar pore to near the antapex along the left margin of the hypocone. The larger masses are found near the distal end of the lens. To the left of the lens and closely associated with it is a long slender body, yellow ochre in color. It may be the homologue of the pigmented core of the more integrated types of melanosome. Its axis is directed anterosinistrally at 15° from the vertical.

The nucleus is just postequatorial, ellipsoidal in shape with no visible chromatin strands in the individual figured. Its major and minor axes are 0.40 and 0.26 transdiameters respectively in length.

A large, club-shaped pusule opens anteriorly into the anterior flagellar pore. A posterior one was not noted. The cytoplasm is clear and finely granular. In the anterior portion of the body and radiating from near the anterior flagellar pore is a group of slender, linear, green rodlets or fluid-filled canals. In the midregion and sparingly elsewhere are small blue-green oil droplets. A large primuline-yellow food mass was present near the ocellus. Thickly scattered in the peripheral plasma are irregular, thin, uniformly distributed vacuoles filled with blue-green fluid. No surface markings or striations were present.

The general color is a pallid methyl blue mottled with the blue-green of the surface vacuoles. The body was surrounded by a close fitting hyaline cyst which during observation became more and more distended in the region of the sulcus, especially over the apical loop.

Dimensions.—Length, 73$\mu$; transdiameter, 54$\mu$; axes of nucleus, 26$\mu$ and 14$\mu$.

Occurrence.—One individual was taken July 25, 1917, 11 miles off La Jolla with a No. 25 silk net in a haul from 80 meters to the surface in a surface temperature of 27°1 C.

Comparisons.—This is the most primitive species of the subgenus *Pouchetia* with diffuse ocellus. Its primitive features are shown in the slight intercingular torsion and in the marked absence of integration in the ocellus as shown in the degree of independence of the elements of the lens and the much divided and widely scattered melanosome. The possibility of disintegration prior to cytolysis is not excluded. As a rule, however, the ocellus resists these disintegrative processes longer than the cytoplasm.

## **Pouchetia purpurata** sp. nov.

Plate 8, figure 87; text figure PP, 3

DIAGNOSIS.—Medium sized species with obovoidal body, widest anteriorly, length 1.75 transdiameters; girdle a descending left spiral of 1.4 turns, displaced 0.48 of the total length; sulcus with apical extension and antapical loop; torsion 1.2 turns; ocellus distributed, postmedian; lens elongated, segmented; melanosome amoeboid, with granular processes; plasma dahlia purple. Length, 88$\mu$. Pacific off La Jolla, California, July.

DESCRIPTION.—The body is obovoidal, wider anteriorly, flattened ventrally, more convex dorsally, its length 1.75 transdiameters measured at the widest part which is about the level of the anterior flagellar pore. The epicone exceeds the hypocone in height by about 0.13 of its own length and is wider and more rotund. Its length at the proximal and distal ends of the girdle is 0.3 and 0.8 respectively of the total length of the body. Its ventral face is somewhat flattened, the dorsal more convex. The apex is subhemispherical. The hypocone is more contracted, its length at the anterior and posterior ends of the intercingular sulcus being 0.7 and 0.2 respectively of the total length. The antapex is rounded and somewhat projected ventrally by the arching of the dorsal side.

The girdle leaves the sulcus 0.3 of the total length below the apex, makes 0.5 turn of a descending left spiral with almost no posterior deflection, steepens rapidly 0.75 turn to 45° and slackens up almost to the horizontal at its distal end of nearly 0.5 turn. It makes a total of 1.4 turns with a total displacement of 0.48 total length, or 0.85 transdiameter. The furrow has a width of 0.08 transdiameter, is not deeply impressed and has a somewhat overhanging anterior lip. The sulcus was not fully determined on the epicone. It appears to start near the apex, curves but slightly in place of the usual apical loop, but runs from apex nearly to the antapex in a fairly uniform descending left spiral with a total torsion of 1.2 turns, 0.6 of which is in an abruptly steepened antapical loop. It is a narrow channel about 0.5 the width of the furrow in the intercingular region, but widens out below in the antapical loop. The flagellar pores are at the junctions of girdle and sulcus and the transverse flagellum runs the whole length of the transverse furrow.

The ocellus is of the diffuse type, postmedian, at the left and close to the distal end of the intercingular sulcus. Its length is unusually great, attaining 0.28 total length of the body, or nearly 0.7 transdiameter. Its greatest diameter is 0.35 of its own length. It lies parallel to the sulcus with the lens directed anterodextrally at an angle of about 35° from the vertical. The lens is hyaline, glaucous green in color with a darker purplish plasma sheath surrounding it and separating its segments. It is a slender shaft of four unequal segments enclosed within a less distinctly differentiated outer sheath. This sheath is incomplete on its sinistral face. The melanosome is more than 0.35 wider than the lens, its main mass forming a stout pitcher-shaped body into which the end of the lens is thrust. From its anterosinistral margin a lobe projects anteriorly and breaks up into an anastomosing, branching network of granular strands of pigment. A disconnected strand of similar granules lies along the anterior lip of the furrow, and several others in the peripheral plasma of the hypocone adjacent to the distal end of the girdle and sulcus.

The nucleus is relatively small. It is an elongated, asymmetrical ellipsoid, located far anterior in the center of the epicone. Its axes are 0.6 and 0.33 transdiameter in length respectively and it is crowded with spirally wound, beaded chromatin threads. A pale ochraceous food ball lies in the center of the very transparent plasma. A cluster of slender, greenish diverging radial rodlets are located in the extreme posterior end, probably metabolic in origin. In the peripheral plasma close to the pellicle are minute, uniformly distributed, greenish droplets.

No pusules were noted. The plasma is a delicate dahlia purple, deepest peripherally and fading a little from the anterior end posteriorly, as though revealing some biochemical axial gradient.

One of the animals seen was enclosed in a roomy, transparent cyst proportioned in contour to the body and filled with a fluid tinged with the color of the organism. Its length was 1.18 that of the body.

DIMENSIONS.—Length, 88μ; transdiameter, 52μ; length of ocellus, 35μ; axes of nucleus, 35μ and 17μ; length of cyst, 95μ.

OCCURRENCE.—The individual figured was taken July 25, 1917, 11 miles off La Jolla with a No. 25 silk net in a haul from 80 meters to the surface in a surface temperature of 21°2 C. It occurred again on July 27 in a haul of similar nature taken 4 miles off La Jolla in a surface temperature of 21°9 C.

ACTIVITIES.—The first individual studied was encysted when found. Under the cover glass, however, it broke out of the cyst and moved quickly across the slide in an almost straight line, with a rapid anticlockwise rotation.

COMPARISONS.—This species belongs to the subgenus *Pouchetia* with diffuse non-integrated ocellus. The lens, in fact, is scarcely organized as an efficient optical organ, and the pigment is distinctly amoeboid and rather widely distributed. In this feature it is near *P. schuetti*, but differs from it entirely in proportions, color, and shape and structure of the lens. In color it is unique in *Pouchetia*, the dahlia purple being of a different tone and darker than the rosy tints of *P. schuetti* and *P. rubescens*. The axial gradation in color from the anterior end posteriorly is not unlike that in *Gymnodinium sulcatum*, *G. rubricauda*, and *Gyrodinium rubrum*, but the reverse of that in *G. postmaculatum*, all species with more or less diffuse reddish to purplish coloration of the plasma (pl. 8, figs. 83, 88, 86, 91).

## **Pouchetia purpurescens** sp. nov.

Plate 8, figure 84; text figure OO, 7

DIAGNOSIS.—Small species with body asymmetrically ellipsoidal, deeply constricted by furrows; length 1.7 transdiameters; girdle forms a descending left spiral of 2 turns, displaced over 0.75 total length; sulcus with short apical loops and torsion of 1 turn; ocellus concentrated, posterior, horizontal, small, apparently at the right of the sulcus; lens spheroidal, melanosome hemispherical, with red central core; plasma amaranth purple. Length, 59μ. Pacific off La Jolla, California, June, July.

DESCRIPTION.—The body is ellipsoidal, asymmetrical at either end, with the posterior portion of the epicone covering the ocellus and forming a projecting lobe. The body is deeply constricted and rendered asymmetrical by the spiral sulcus. The epicone and hypocone are nearly equal. The epicone is small at its anterior end with a length of 0.06 of the total length of the body at the proximal end of the girdle. From this point it sweeps around the body posteriorly in a broad band about 0.55 transdiameter in width, which terminates at a distance from the antapex of 0.1 of the total body length. The apex is broadly rounded. The hypocone follows the epicone in its course around the body with a slightly broader band which terminates in a button-shaped

eminence at the antapex. The antapical region is grooved ventrally by the sulcus, which forms a deep trough, to the right of which the hypocone swells out to a broad, slightly rounded lobe, asymmetrically placed at the right of the shallow sulcal notch in the postmargin.

The girdle at its proximal end is distant 0.06 of the total length of the body from the apex. It curves around dorsally in a horizontal semicircle before beginning its posterior direction in a steep descending left spiral 60° from the horizontal. It makes two complete turns around the body and joins the sulcus distally 0.1 of the length of the body from the apex, flattening the spiral again to the horizontal gradually in the last 0.75 turn. Its displacement thus equals 0.84 of the length of the body. The furrow is deeply impressed and is 0.1 transdiameter in width. The anterior flagellar pore opens at the junction of the girdle and sulcus. The transverse flagellum traverses one-half the entire length of the girdle. The posterior flagellar pore is found at the distal junction of the sulcus and the girdle. Both pores open on the ventral face.

The sulcus invades the epicone half the short distance to the apex. It makes one complete revolution of the body in a uniform steep descending left spiral as a narrow channel in a deep furrow, widening distally, and beyond the flagellar pore spreading out as a broad trough, one side of which partly encircles the distal eminence of the hypocone, forming a broad notch in the outline of the body viewed dorsoventrally.

The ocellus is of the concentrated type. It is situated 0.25 of the total length of the body from the posterior end on the *right* of the distal end of the sulcus instead of the left, as usual in *Pouchetia,* occupying a somewhat protruding, posterodextral portion of the epicone. Its length is almost 0.25 transdiameter and its axis is horizontal with the lens directed to the left. In a second individual it was directed anterodextrally 45° from the horizontal. It is composed of a hemispheroidal melanosome with a brilliant red central core, partly surrounding the base of the simple spheroidal lens of about the same size as the melanosome. The lens is a clear, hyaline, asymmetrical sphere with faint indications of concentric layers and the melanosome is without indications of amoeboid processes. In a second individual of larger size the melanosome was flattened and twice the diameter of the somewhat elongated lens. Both lens and melanosome were less symmetrical than in the individual figured. As cytolysis approached the lens flattened into a disc with an axial button.

The ellipsoidal or spheroidal nucleus is situated near or somewhat posterior to the middle of the body. It is ellipsoidal in shape in the individual figured with major and minor axes of 0.6 and 0.4 transdiameter respectively. Chromatin strands follow its major axis.

No pusules were noted in the encysted individuals examined. The cytoplasm is clear or finely granular with few or many larger granules and oil globules. The individual figured showed no granulations or vacuoles and but one large, rounded, ochraceous food mass enclosed in a vacuole.

The surface of the body presents no striations or other markings and there are no peripheral vacuoles. In one individual, as cytolysis approached, minute lines and lenticels of colored fluid gathered in the peripheral plasma with some indications of a longitudinal linear order 10–12 across one face. The color is amaranth purple diffused through the cytoplasm. The color may become aggregated into small blotches or into strands or threads peripherally located as above noted, leaving the adjacent cytoplasm colorless. Both individuals examined were contained in thin, hyaline, close fitting cysts.

DIMENSIONS.—Length, 59–68$\mu$; transdiameter, 35–39$\mu$; axes of nucleus, 22–27$\mu$ and 16–22$\mu$; length of ocellus, 9$\mu$; its greatest width, 7.5$\mu$.

ACTIVITIES.—Both individuals examined showed no active movements beyond continuous vibrations of the transverse flagellum without rotation within the cyst.

Occurrence.—One individual was taken from the surface haul made with a No. 12 silk net at the end of the pier at the Biological Station at La Jolla, California, on June 7, 1917, in surface temperature of 17°3 C, and the other from a haul made 4 miles offshore with a No. 25 silk net on July 11, 1917, from a depth of 80 meters to the surface and in a surface temperature of 19°7 C.

Comparisons.—The purplish color of the plasma somewhat resembles that of *P. purpurata* and *Gyrodinium postmaculatum*, although the species *P. purpurescens* has little else in common with either of these species. *P. fusus* is the only species equaling it in the amount of torsion (2 turns) of the girdle and sulcus combined. The location of the ocellus at the right of the sulcus instead of the left is unparalleled in the genus *Pouchetia*. This species was particularly puzzling and difficult to interpret because of the uncertainties in following the girdle and sulcus. There is here a possibility of a mistaken interpretation. Assuming a correct interpretation, it appears that the ocellus has been crowded from an internal position at the left side of the posterior part of the intercingular sulcus to the right side without very marked change in either position or direction of its axis. This might be due to the crowding of food balls ejected before encystment. The location of the ocellus was the same in a second encysted individual, but its axis was turned anteriorly 45°. Since we have little evidence that the ocellus is subject to marked changes in position in the cytoplasm the suggestion that this ocellus has been shifted by pressure into an unusual position from the normal and expected one must be regarded as tentative.

This species is a moderately specialized member of the subgenus *Pouchetiella* with integrated lens, as shown by the small and variable ocellus, high coloration, and extreme torsion of the girdle and sulcus.

### **Pouchetia rosea** (Pouchet) emend.

Text figure OO, 4

*Gymnodinium polyphemus* var. *roseum* Pouchet (1897), pp. 93, 96–97, 112, pl. 10, fig. 1.

Not *Pouchetia rosea*, Schütt (1895), pp. 94, 95, pl. 26, fig. 92 (= *P. schuetti* nom. sp. nov.).

*P. rosea*, Lemmermann (1899), p. 360. In part, includes *P. schuetti*.

*P. rosea*, Schröder (1900), p. 14. Based on Schütt's figures (1895) (= *P. schuetti*).

*P. rosea*, Pavillard (1905), p. 48, pl. 3, fig. 4. Schütt's *P. rosea* (1895) regarded as problematical.

*P. rosea*, Paulsen (1907), p. 24; (1908), pp. 105, 106, fig. 146. In part, tentative inclusion of Schütt's *P. rosea* (1895).

*P. rosea*, Ostenfeld (1913), pp. 338, 358, 476. Allocation indeterminable.

Not *Gymnodinium roseum*, Dogiel (1906), pp. 20–26, pl. 2, figs. 26–37 (= *Chytriodinium roseum* (Dogiel) Chatton (1912), pp. 91–92).

Not *Gymnodinium roseum*, Lohmann (1908), pp. 202, 252, 366, 368, tab. B, pl. 17, figs. 24–28 (= *G. lohmanni* Paulsen (1908), p. 99, figs. 137 A–D).

Diagnosis.—A small species with irregularly ellipsoidal body, its length 1.3–1.66 transdiameters; girdle a descending left spiral of at least 1.25 turns, displaced about 0.5 total length; sulcus with less than 0.5 turn; ocellus with elongated lens and red pigment mass. Length, 44–58μ. Atlantic at Concarneau; Mediterranean at Cette; April, October.

Description.—This is based on Pouchet's (1887) and Pavillard's (1905) figures. The body is irregularly ellipsoidal, with protuberant girdle when free, rounded up when encysted; its length 1.66 (1.3) transdiameters. The epicone and hypocone are subequal. Its altitude at the proximal end of the girdle is about 0.33 of the total length and over 0.66 at the distal end. The apex is broadly rounded. The antapex of the hypocone is broadly rounded in the cyst, asymmetrical and longer on its left side in the free state. In the lower one of Pouchet's (1887) two figures the postmargin is obliquely truncate and the body lacks the food ball present in the upper figure. Pouchet states, however, that they represent two individuals. A similar truncate appearance follows the extrusion of food balls at the antapex in other species.

The girdle appears to make about 1.5 turns in Pouchet's figures, but is not completely portrayed in Pavillard's. Its displacement is at least 0.5 the length of the body. The furrow is deeply impressed with protuberant lips in the free state.

The sulcus extends (?) a short distance on the epicone, and continues as a narrow groove in a spiral course of 0.25 to 0.50 turn to the postmargin.

The ocellus is of the concentrated or simple, more integrated type. It lies at the left of the posterior part of the intercingular sulcus with its axis directed anterodextrally at about 50° from the horizontal. Its length is 0.40 to 0.45 transdiameter. It consists of an elongated lens imbedded at one end in a flattened hemispherical bright red pigment mass. In Pouchet's figure the pigment is light rose, in Pavillard's scarlet with darker margin. In the former the lens is swollen distally and its exposed length equals the diameter of the pigment mass. It shows no lamellae. In Pavillard's figure it is 0.65 of the diameter of the pigment mass in length, not swollen distally, and has several transverse lamellae.

The nucleus lies anteriorly in the epicone, is ellipsoidal in form with its major and minor axes 0.75 and 0.50 transdiameter in length respectively and oblique to the axis of the body. It contains fine parallel chromatin threads. An orchraceous food ball or a vesicle filled with a fluid colored by diatomin is figured by both Pouchet and Pavillard. The former states that the plasma is completely hyaline with a yellowish tint locally. It is not rosy as figured by Schütt (1895) in the forms he refers to this species.

Dimensions.—Length, 44 (58)μ; transdiameter, 25 (46)μ; diameter of nucleus, 17 (34)μ; length of ocellus, 10 (22)μ. Pouchet states that the length of the body is 30μ; but the figure measures 44μ on the basis of the stated magnification, 500 diameters. The dimensions in brackets are of Pavillard's figure.

Occurrence.—Two individuals with red pigment mass were taken in a haul of a No. 12 silk net from 120 meters to the surface on July 7, 1904, about 10 miles southwest of Point Loma, California, in surface temperatures of approximately 17°–18° C. Their lengths were 45μ and 50μ and transdiameters 24μ and 30μ respectively.

Originally described by Pouchet (1887) from the plankton of the Atlantic at Concarneau, France, where he discovered it on March 25, and at a later visit on April 23 to 26. The only other record which can be assigned critically to this species is that of Pavillard (1905), whose figure bears a marked similarity to Pouchet's original sketches and has the red pigment mass as originally

described and figured. Pavillard (1905) records *P. rosea* as rare in the plankton of the Etang de Thau at Cette, France, on the Mediterranean in October, 1904. Surface temperatures during this month ranged from 18.4 C to 13.9 C.

The only records which can be considered as possibly including *P. rosea*, as here delimited, are those of Paulsen (1907) and Ostenfeld (1913) which refer to specimens seen by the latter in plankton from the North Sea off Tyborn, Denmark, in March and April, 1900, and from the Cattegat in May, 1898. Their status is, however, not critically determinable.

Comparisons.—This is the only species in the genus *Pouchetia* with a red pigment mass instead of the usual black melanosome. The relatively slight torsion of the body, about 0.25 turn, the red instead of black pigment and elongate laminate lens indicate that this is one of the simpler species of the subgenus *Pouchetiella*.

The differences between the figures of Pouchet (1887) and Pavillard (1905) are considerable. Pouchet's has a length of 44μ, Pavillard's of 58μ. The former is 1.66 transdiameters, the latter 1.3 in length. The lens expands distally in the former and does not in the latter; the former is somewhat angular, the latter rotund. These differences are possibly referable to the fact that Pouchet's specimen was not encysted while Pavillard's was in a cyst and apparently well rounded up. The upper one of Pouchet's figures (both are turned upside down) has an expanded truncate postmargin. This suggests that it had recently disgorged a food ball such as is seen in the lower figure (compare our fig. 61, pl. 6) of *Pouchetia maxima*, which has a similar antapical margin and had recently discharged a food mass.

Synonymy.—Originally described by Pouchet (1887) as *Gymnodinium polyphemus* var. *roseum*, but transferred to *Pouchetia* by Schütt (1895), who applied the name to an assemblage of at least two species different from Pouchet's. The synonymy of this species is full of perplexities arising from the inadequacy of Pouchet's (1887) original account and figures, from his relating of his form to his *G. polyphemus* as a variety, and from Schütt's allocation in *Pouchetia rosea* (Pouchet) of what appear to us to be two distinct species, neither of which is referable in our opinion to Pouchet's original *P. roseum*. There is also, at present, lack of adequate and critical knowledge of the limits of variability within the species of this group and of the pathological changes which the constituent parts of the ocellus may undergo. It is also possible that encystment may modify the condition and appearance of the ocellus.

In view, however, of the structural features involved in speciation in this genus as a whole we have arrived at the following tentative solution of the perplexities surrounding this species:

1. Pouchet's *Gymnodinium polyphemus* var. *roseum* (1887) is a distinct species, *Pouchetia rosea* (Pouchet), but not *P. rosea* (Pouchet) Schütt or *Gymnodinium roseum* Dogiel or *G. roseum* Lohmann. It is not Pouchet's *G. polyphemus* (1885*b*).

2. Schütt's (1895) *Pouchetia rosea* (Pouchet) is a complex of forms none of which is Pouchet's species, *P. rosea*. One of these (Schütt's, pl. 26, figs. $92_{3-12}$) has the diffuse or compound type of ocellus with divided lens and branching, amoeboid pigment mass. To this we assign the new name *Pouchetia schuetti*. The other and smaller form (Schütt's, pl. 26, figs. $92_{1-2}$) with a length of 70–59$\mu$ as compared with 87$\mu$ in the first group has a concentrated or simple lens and a solid melanosome. This appears to be a mutilated or contracted individual, possibly moribund. The possibility of a distinct species is not precluded. We leave it as indeterminable, but probably not *P. schuetti* sp. nov.

The synonymy of the citations of *Pouchetia rosea* (Pouchet) Schütt recorded by workers subsequent to Schütt (1895) is a matter which cannot be determined beyond the point of noting their inclusive nature, since none of them has critically compared his material with the figures of Pouchet and Schütt, though Pavillard (1905), Paulsen (1908), and Ostenfeld (1913) have all noted the perplexing status of *P. rosea* (Pouchet) Schütt.

Lohmann (1908) describes as *Gymnodinium roseum* a new species which Paulsen (1908) later renames *G. lohmanni* because of the preoccupation of the name *roseum* by Dogiel's (1906) *G. roseum*. Both Lohmann's and Dogiel's names are, however, excluded from *Gymnodinium* because of Pouchet's *Gymnodinium polyphemus* var. *roseum* (1887). Dogiel's *G. roseum* is utilized by Chatton (1912) as the type species of a new genus *Chytriodinium*.

## **Pouchetia rubescens** sp. nov.

Plate 8, figure 90; text figure OO, 5

Diagnosis.—Medium sized species, obovoidal, length 1.4 transdiameters; girdle a descending left spiral of 1.2 turns, displaced 0.5 transdiameter; sulcus with apical loop much displaced ventrally, antapical section short; torsion 1.2 turns; ocellus concentrated, posterior; lens hemispherical; pigment mass hemispheroidal, dark brown; color, pink. Length, 73$\mu$. Pacific off La Jolla, California, July.

Description.—The body is slightly obovoidal, with its widest transdiameter 0.32 of the total length from the anterior end. The epicone is 0.3 longer than the hypocone, with hemispherical apical contour notched at the ventral side of the apex by the sulcus. Its length above the anterior flagellar pore is 0.4 and from its posterior extremity is 0.9 of the total length of the body. The hypocone is contracted somewhat, bulging ventrally between the furrows, somewhat flattened ventrally towards the antapex and slightly grooved by the distal end of the sulcus. Its length from its anterior termination to the antapex is 0.5 and from the distal junction of the girdle and sulcus 0.07 of the total length of the body. The antapex is rounded without sulcal notch.

The girdle meets the sulcus at a point 0.46 of the total length of the body from the apex, passes thence around the body 0.3 of a turn before sweeping posteriorly in a descending left spiral, steepening to 35° from the longitudinal to join the sulcus at a point 0.09 of the total

length of the body from the antapex. It lies in a broad, deep depression, and has a width of 0.06 transdiameter and is bordered by overhanging lips. The anterior flagellar pore is located at the proximal junction and the posterior pore at the distal junction of the girdle and sulcus. The transverse flagellum traverses approximately the entire length of the furrow.

The sulcus forms a wide loop above the anteroir flagellar pore, curving over the top of the epicone just ventral to the apex and terminating midway between that and the girdle. It is deeply imbedded like the girdle throughout its entire length, the lips forming high overarching ridges. Below the anterior flagellar pore it sweeps around for 0.5 turn before joining the distal end of the girdle, beyond which it passes to the antapex directly without antapical loop. Its total torsion is about 1.2 turns, but the spiral course is obscured by the ventral deflection of the apical loop.

The ocellus is located far anterior at the left of the distal end of the intercingular sulcus close to the posterior flagellar pore. Its length is 0.37 transdiameter and it is directed antero-sinistrally at about 45° from the vertical. The ocellus is of the concentrated type with subequal hemispheroidal lens and pigment mass. The lens is laminated, with three equidistant hyaline laminae, bluish in color. Closely imbedding its base is the pigment mass of dark brownish black pigment enclosing the central core of a lighter brown tone.

The nucleus is ellipsoidal and located dorsally slightly in front of the equatorial plane. Large chromatin strands follow the course of its major axis. Its axes are 0.57 and 0.40 transdiameter in length respectively.

The cytcplasm is finely granular, containing only a few oil globules in the midregion. Two cinnamon rufous food masses were present in the individual figured. No pusules were observed. Neither surface markings nor striations were present.

The color is a mottled pink distributed through the cytoplasm, occasionally showing a noticeable granular appearance. In the specimen figured three small, rose-red globules of pigment were found in the periphery in the equatorial region. The organism was enclosed in a large, ovoidal, thin, hyaline cyst 1.28 lengths of the body in length.

An encysted individual (fig. P, 1) was also present in the haul on July 2, 1917, which, from its size, color, and type of ocellus, we place in this species. The body had rounded up into a sphere, with a central, spherical nucleus, peripheral hemispherical pigment mass, with adjacent, detached, partially disintegrated lens. It was immediately surrounded by a delicate, close fitting film, outside of which, as a cap covering nearly two-thirds of the sphere, was a degenerating, cytoplasmic cap containing local aggregates of brownish pigment. The whole was enclosed in an oblong hyaline outer cyst over twice the diameter of the sphere in length. It appears that the encysting animal must have shed off or extruded a considerable mass of plasma containing pigment between the formation of the outer and inner cysts.

DIMENSIONS.—Length, 50–73$\mu$; transdiameter, 25–50$\mu$; axes of nucleus, 25–30$\mu$ and 15–21$\mu$; length of ocellus, 9–18$\mu$; length of cyst, 94$\mu$; its transdiameter, 70$\mu$.

OCCURRENCE.—Two specimens, both encysted, were taken on July 2, 1917, 6 miles off La Jolla, California, with a No. 12 silk net in a haul of 60 meters to the surface and in a surface temperature of 21°9 C. It occurred again on August 15 in a haul taken 0.75 mile off La Jolla, California, with a No. 25 silk net from 80 meters to the surface in a temperature of about 22°5 C.

COMPARISONS.—*Pouchetia rubescens* is a typical representative of the subgenus *Pouchetiella* with highly integrated ocellus, in the case of both the lens and pigment mass. It is near *P. subnigra*, but differs from it in several features. The length of the epicone at the proximal end of the girdle in *P. subnigra* is 0.3 and in *P. rubescens* is 0.45 length of the body and the apical loop of

the latter crosses the apex while it curves dorsally below it in the former. The lens is elongate in *P. subnigra* and hemispherical in *P. rubescens*. They differ also in proportions and size of body.

## **Pouchetia schuetti** nom. sp. nov.

Text figures PP, 10, 11

*Pouchetia rosea* (Pouchet) Schütt (1895), pp. 95, 96, 169, pl. 26, fig. $92_{1-12}$. Figure $92_{11}$, marked $93_4$ on plate.

*P. rosea,* Lemmermann (1899), p. 360. In part.

*P. rosea,* Schröder (1900), p. 14.

*P. rosea,* Pavillard (1905), p. 48, pl. 3, fig. 4. This is *P. rosea* (Pouchet).

*P. rosea,* Paulsen (1907), p. 24; (1908), pp. 105, 106, fig. 146. In part, includes *P. rosea* Pouchet.

Diagnosis.—A medium sized species of asymmetrical ovoidal form, expanded posteriorly, its length 1.4 transdiameters; girdle a descending left spiral of 1.25 turns, displaced nearly 0.5 transdiameter; sulcus with about 1.5 turns, with apical and antapical loops; ocellus dispersed with lens of five segments and black, dendritic, amoeboid melanosome, plasma rosy. Length, 70–87$\mu$. Atlantic, Mediterranean.

Description.—This is based on Schütt's (1895) figures $92_{3-12}$, explanations of figures, and brief textual references. The body is asymmetrically and irregularly ovoidal, flattened ventrally, convex dorsally, and expanded posteriorly. Its length is 1.4 transdiameters and the dorsoventral diameter is 0.9 of the transdiameter. The epicone is longer than the hypocone and perhaps larger. Its apex is rounded and more convex dorsally than ventrally, and, in ventral view, somewhat flattened transversely. Its lengths at the proximal and distal ends of the girdle are 0.6 and 1 transdiameter respectively. The hypocone is more distended, very convex posterodorsally and excavated ventrally, the sulcal notch being carried up ventrally and to the right.

The girdle begins a little anterior to the middle of the body, makes an even descent of a full turn of a descending left spiral, steepens distally rather abruptly as it joins the sulcus, completing in all at least 1.25 turns. Its distal end is only about 0.2 transdiameter from the postmargin. The furrow is about 0.06 transdiameter in width with well marked lips. The sulcus is not fully delineated but runs from the middorsal region of the epicone posteriorly to the right postmargin with a torsion of nearly 1.5 turns. The apical loop above the girdle extends 0.5 turn upon the epicone, the intercingular torsion is about 0.25 turn, and the antapical loop below the posterior flagellar pore is deflected to the right, where it probably makes about 0.75 of a turn (fig. $92_{11}$). The whole sulcal region is somewhat deeply impressed into the body. The transverse flagellum fills the whole length of the girdle. The longitudinal one arising from the pore at the junction of the posterior end of the girdle and the sulcus is about 0.5 transdiameter in length.

The ocellus is of the dispersed or non-integrated type. It lies at the left of the intercingular sulcus near its posterior end and very near the posterior end of the body. Its total length is about 0.45 transdiameter, and its axis is directed anterodextrally at an angle of about 20° from the vertical. It consists of an elongated, segmented, hyaline lens of five appressed parts in a linear series or loosely assembled. Posterior to these and somewhat enveloping them is a black, amoeboid melanosome of irregular shape, which during observation spread out into branching lobed amoeboid processes reaching from the girdle to the antapex in the peripheral plasma. No colored core was noted.

The nucleus is a broadly reniform structure in the left middorsal region. Its major and minor axes are respectively 0.8 and 0.45 transdiameter in length. It is traversed lengthwise by fine crowded chromatin threads. No pusules were noted. A large ochraceous food ball lies in the center of the hypocone near the nucleus. The plasma is rosy from peripheral, anastomosing erythrosomes which in the moribund state round up into spheres of fairly uniform size and distribution, somewhat in lines, in the peripheral plasma which is elsewhere colorless. Among these are found elliptical, reniform and slipper-shaped leucoplatysomes, 0.10 to 0.14 transdiameter in length.

Schütt's specimens were each enclosed in a transparent, hyaline cyst somewhat larger than the body. In the case of one of the individuals (fig. $92_{1-2}$) the cyst wall was double-contoured, more closely applied and a second cyst wall was detaching itself on the ventral face. This individual was evidently moribund, much rounded up as a whole with the rosy pigment of the plasma concentrated into the so-called erythrosomes and the pigment mass of the ocellus retracted into a compact, flattened disk. It is also probable that the lens which in figures $92_{3-12}$ is erect is here thrown down against the contracted melanosome.

The small spherical cyst attached at the posterior end and filled with leucoplatysomes and an erythrosome is evidently a fragment of the body encysted separately but still adherent to the parent plasma. The extrusion of a food ball at the posterior margin might be the cause of such a detachment and, because of the withdrawal of substance, of the dislocation of the lens also.

Dimensions.—Measurements of figures $92_{1-2}$ in parentheses. Length, 87 (70, 59)$\mu$; transdiameter, 54 (45, 50)$\mu$; length of ocellus in axis, 30 (13)$\mu$; diameter, 10–21 (25)$\mu$.

Occurrence.—Schütt (1895) gives no data, but his material may have come from the Bay of Naples or have been seen on the Plankton Expedition in the Atlantic.

Comparisons.—The possibility of two separate species being represented by the two sets of figures (figs. $92_{1-2}$ and $92_{3-12}$) is not excluded, but in view of the possible abnormality of the individual represented in the first group, as above indicated, it seems best to leave these *in statu quo* and base the species on the second group of figures with the interpretation of the others as divergent or abnormal representatives.

The species as thus defined is a member of the subgenus *Pouchetia* with diffuse or non-integrated ocellus. It is, in fact, less integrated than any other species of *Pouchetia*, being nearest to *P. poucheti*, where the pigment is scattered and the lens deeply lobed. The amoeboid pigment is less markedly developed in *P. subnigra* (fig. OO, 6), *P. alba* (fig. PP, 8), *P. atra* (5), and *P. purpurata* (3), in all of which are fine lines of granules forming a feebly developed network spreading from the central pigment mass. Segmentation of the lens is evident also in *P. alba*, *P. atra*, and *P. purpurata*, in which there are no black pigment processes, but instead scattered lines of red granules.

The lack of extreme torsion in the intercingular region of the sulcus and the diffuse structure of the ocellus are indications of a generalized or less advanced stage of development of this species, while the high differentiation of the terminal loops of the sulcus points towards specialization.

Synonymy.—This species includes tentatively all of the forms figured by Schütt (1895) and, by implication resulting from the citations by the authors

named, of the figures both of Pouchet (1887, = *P. rosea* (Pouchet) and of Schütt (1895) only a part of *P. rosea* as reported by Lemmermann (1899), Pavillard (1905), and Paulsen (1907, 1908). *P. rosea* Dogiel (1906) is *Chytriodinium roseum* (Dogiel) Chatton (1912) and *P. rosea* Lohmann (1908) is *P. lomanni* Paulsen (1908). *P. rosea* of Schröder's (1900) reference is exclusively *P. schuetti.*

## **Pouchetia striata** sp. nov.

Text figure OO, 8

Diagnosis.—Body rotund, length 1.2 transdiameters; girdle a descending left spiral of 1.2 turns, displaced 0.48 transdiameter; sulcus with anterior and posterior loops and a torsion of 1 turn; ocellus concentrated, posterior; lens ellipsoidal; melanosome hemispherical, black with red core, color rose red; surface coarsely striate. Length, 75$\mu$. Pacific off La Jolla, California, August.

Description.—The body has a robust habit, its length exceeding its transdiameter by only 0.2. The epicone exceeds the hypocone in length by 0.25. The epicone is broad, contracting below the equator, with subhemispherical apex, with a length on the left of the sulcus of 0.46 and on the right of 0.8 of the total length of the body. The hypocone is more contracted than the epicone, obliquely flattened on the left side where the distal end of the sulcus makes a broad trough which extends down to the subhemispherical antapex.

The anterior junction of the girdle and sulcus occurs at 0.46 of the total length of the body from the apex. The girdle follows a descending left spiral course around the body and meets the sulcus distally at about 0.8 of the total length of the body from the apex. The furrow is 0.08 transdiameter in width and is deeply impressed with smooth, overhanging borders. The anterior flagellar pore is located at the anterior junction of the girdle and sulcus and the posterior pore slightly below the posterior junction.

The sulcus extends anteriorly around the epicone in a wide loop which terminates at the apex, making 0.5 turn above its anterior junction with the girdle. Below this it passes posteriorly at an angle of about 40° from the horizontal to meet the girdle distally, below which it turns abruptly posterior to the antapex. It forms a wide, shallow trough with smooth borders. Below the posterior junction of girdle and sulcus it broadens, resulting in an oblique flattening of the left side of the antapex. There is no antapical loop.

The ocellus is 0.45 transdiameter in length, posteroventrally located at the left of the distal end of the intercingular sulcus. It is directed anterosinistrally at an angle of about 20° from the vertical. The clear hyaline lens is ellipsoidal, about 0.35 transdiameter in length and 0.22 in diameter and has three concentric laminae. The posterior portion is imbedded in the melanosome, which is black, hemispherical, with undulating contour, and has a red central core.

The nucleus is large, spheroidal, and located in the anterosinistral region. Its axes are 0.56 and 0.52 transdiameter in length respectively.

The cytoplasm is very clear and transparent. Centrally located near the ocellus was a rounded food mass and several refractive, colorless oil globules. The cytoplasm in the interior of the body is colorless with the characteristic rose-red color of the organism concentrated in the peripheral layer. The surface of the body is striate with a few equidistant, longitudinal, bluish green lines, five or six across one face. These are found on both hypocone and epicone, but fade out near the apices and girdle.

DIMENSIONS.—Length, 75μ; transdiameter, 62μ; axes of nucleus, 35μ and 32μ.

OCCURRENCE.—A single individual was taken August 21, 1917, with a No. 25 silk net, 5 miles off La Jolla, California, in a haul from 83 meters to the surface and in a surface temperature of 22°5 C.

COMPARISONS.—This species is a typical member of the subgenus *Pouchetiella* with concentrated ocellus. It is close to *P. voracis*, but has a more highly perfected ocellus, especially with reference to the lens. The epicone is higher, the displacement less, and torsion greater than in *P. voracis,* which also lacks the longitudinal striae characteristic of this species. The only other species in *Pouchetia* with longitudinal striae are *P. violescens* and *P. maxima*, both extremely large species. *P. voracis* has, however, no close affinities with either of these species. It is the most nearly spherical of all species of *Pouchetia.*

### **Pouchetia subnigra** sp. nov.

Plate 6, figure 66; text figure OO, 6

DIAGNOSIS.—Body large, ovoidal, length 1.6 transdiameters; girdle a descending left spiral of 1.3 turns, displaced 0.6 transdiameter; sulcus with anterior and posterior loops; torsion 1 turn; ocellus concentrated, posterior lens; elongated, laminate black melanosome with brown, central core. Length, 101μ. Pacific off La Jolla, California, July.

DESCRIPTION.—This large species has an irregularly ovoidal body with its widest transdiameter near the equatorial plane. The epicone is somewhat larger than the hypocone. Its apex is broadly rounded, deeply grooved on the dorsal and left faces by the anterior loop of the sulcus. Its length above the anterior flagellar pore is 0.2 and from its distal extremity is 0.8 of the total length of the body. The hypocone is much narrower, approaching subconical, with rounded antapex. This is slightly notched on the ventral face by the distal end of the sulcus.

The girdle joins the sulcus 0.3 of the total length of the body from the apex. It sweeps around the body in a uniform descending left spiral, making 1.3 turns and meeting the sulcus distally at a point 0.17 of the total length of the body from the antapex, giving it a displacement of 0.6 transdiameter. The anterior flagellar pore is located at the anterior junction of the girdle and sulcus, the posterior pore near the posterior junction. The transverse flagellum traverses 0.7 of the total length of the furrow which is deeply impressed.

The sulcus invades the epicone in a wide loop, making 0.6 turn and partly encircling the apex. It forms a broad, rather deep trough, which indents the outline of the epicone. Its lips are smooth and rounded. After its anterior junction with the girdle it narrows to about 0.5 of its width anteriorly and proceeds posteriorly as a rather shallow trough in a depression. It makes 0.4 turn before joining the girdle distally, after which it invades the hypocone as a short loop which notches the ventral face of the hypocone.

The ocellus is large, 0.58 transdiameter in length, ventrally located, slightly posterior to the equatorial plane at the left of the posterior end of the sulcus. Its axis is longitudinal and the lens is directed anteriorly. The concentrated, laminated lens is pale bluish in color, oblong, subovoidal, slightly asymmetrical in outline and has its base imbedded in the melanosome. The melanosome is black with brown central core, large and irregularly rounded in outline, with long, slender, granular, amoeboid strands extending out from it into the protoplasm. These strands cross and form a kind of loose, open-meshed network close to the surface ventrally and posteriorly. Other disconnected strands are found along the dorsal borders of the girdle and of the sulcus beyond the anterior flagellar pore.

The nucleus is large, elongated ellipsoidal, with no visible chromatin threads. It is located near the central part of the body, its major axis nearly parallel to the major axis of the body. Its major and minor axes are 0.88 and 0.40 transdiameter in length respectively.

The protoplasm is finely granular with no food inclusions or oil globules in the specimen figured. No pusules were noted. The color when first observed was rose pink diffused through the protoplasm. After some minutes under the cover glass the color collected in small globules, as figured in plate 6, figure 66, leaving the surrounding protoplasm with a yellowish tinge. No surface markings or striae were detected. Both individuals were enclosed in a thin, hyaline cyst when first observed.

DIMENSIONS.—Length, 101μ; transdiameter, 63μ; axes of nucleus, 50μ and 28μ.

OCCURRENCE.—Two individuals were taken July 7, 1904, with a No. 20 silk net in a haul from 82 meters to the surface, 11 miles southwest of Point Loma, California. Surface temperatures in July in this region range from 19° C to 21° C.

ACTIVITIES.—The flagella continued to be active within the cyst during observation. Shortly before cytolysis the animal began to rotate very rapidly within the cyst and then its diffuse, rosy pigment collected in globules regularly distributed in the peripheral plasma.

COMPARISONS.—This is a member of the subgenus *Pouchetiella* with integrated ocellus, but the integration is not complete, since there is still an amoeboid network of pigment. This is, however, slight in total amount, although of wide extent, and does not seem to detract from the structural and functional efficiency of the ocellus. The ocellus is of the elongated type with concentric laminations. Other elongated lenses as in *P. purpurata, P. schuetti,* and *P. maculata* are transversely segmented.

This is the largest of the species of *Pouchetia* with posterior ocellus, and shares with others of that group the slight development of the antapical loop of the sulcus. The large size, integrated ocellus, large apical loop and high coloration are all indicative of the high specialization of this species.

## **Pouchetia violescens** sp. nov.

Plate 11, figures 118, 120; text figure OO, 1

DIAGNOSIS.—A large species; body ovoidal, length 1.8 transdiameters; girdle a descending left spiral of 1.5 turns, displaced 0.66 transdiameters; sulcus with apical and antapical loops with torsion of 3 turns; ocellus of concentrated lens and black pigment with lighter core; color, violet. Length, 115μ. Pacific off La Jolla, California, June, July.

DESCRIPTION.—This is a large species with stout, ovoidal body, with its widest transdiameter at the proximal base of the epicone somewhat anterior to the middle of the body. The epicone greatly exceeds the hypocone in both length and volume. The epicone is long and domelike with rounded apex notched by the anterior loop of the sulcus. Its length above the anterior flagellar pore is 0.4 and from its distal end is 0.8 of the total length of the body. Below the anterior pore it narrows down to a point in 1.5 turns. The hypocone is narrower than the epicone and has the shape of a truncated cone of about 75°. It is deeply excavated in the region of the lens, and its antapex is obliquely truncated.

The girdle joins the sulcus at a point distant from the apex 0.4 of the total length of the body. It sweeps around the body in a descending left spiral and after 1.5 turns meets the girdle 0.2 of the total length of the body from the antapex. It occupies a broad, deep depression with smoothly rounded borders. The anterior flagellar pore is situated at the point of its anterior junction with the sulcus and the posterior pore slightly below the posterior junction on the opposite face of the body from the anterior pore. The transverse flagellum traverses about 0.5 of its length. In figure 118, plate 11, the flagellum was inverted and occupied the anterior portion of the sulcus. In figure 120 and text figure OO, 1, it is found occupying its normal position on the girdle.

The sulcus invades the epicone in a wide loop of 1.5 turns above the anterior junction with the girdle. It passes once around the body and then turns upward and abruptly to the left, ending on the apex which it notches. Below the anterior pore it turns in a descending left spiral course, making 0.5 turn before meeting the distal end of the girdle. Beyond this it makes one complete turn around the antapex, ending on the left side. The sulcus occupies a rather broad and deep channel throughout its course except where passing over the ocellus below the anterior pore. Here it becomes somewhat obscured by the projecting body of the pigment mass.

The ocellus is large and situated immediately below the proximal part of the girdle near the middle of the body and on the left of the sulcus, and is directed dorsoventrally or postero-anteriorly. Its length is 0.42 transdiameter and its axis is subhorizontal, raised 20° above the horizontal and pointed to the left in one specimen (pl. 11, fig. 118) and deflected posteriorly an equal amount or more in a second (moribund) individual. The lens is large, spherical, with concentric laminae of a clear, hyaline material. It is slightly imbedded in the pigment mass. The melanosome is generally larger than the lens, actively amoeboid and black in color with a lighter central core. In figure 118, plate 11, the lighter central core is seen emerging from the black pigment mass as a large clear body just above the mass of pigment which is here rounded up, and pressing close against the lens. In this same figure the line of sulcus across this region is not shown and one small arc of the outer wall of the lens is omitted by oversight. In text figure OO, 1, the details of this area are complete. In figure 120, plate 11, another individual is shown in which the amoeboid melanosome has moved farther anteriorly around the lens. Since this is seen here from the melanosome end its length is foreshortened and the relations of lens and melanosome somewhat obscured.

The nucleus is large, spheroidal and is located in the anterior half of the body. About thirty-five fine parallel beaded chromatin threads traverse it obliquely. Its diameter is 0.27 transdiameter of the body. A large, bifurcating pusule filled with pinkish fluid passes into the center of the body from the anterior flagellar pore and a smaller sacklike one trends posteriorly from the same region. On one face six to eight nearly equidistant striae, interrupted by the ocellus, are found in the peripheral plasma.

The cytoplasm is very clear and transparent. A few refractive oil drops and a single large, ochraceous food mass were found close behind the ocellus in figure 118. A few minute, bluish green oil droplets were scattered through the peripheral plasma. The color is a clear, light violet, diffused somewhat uniformly throughout the peripheral zone of cytoplasm. The individual drawn in figure 120, plate 11, showed the same diffuse distribution of the color as in figure 118 when first observed. After being kept under the cover glass for nearly one hour the color began to condense into small granules and longitudinal lines, especially along the girdle, which formed a mesh over parts of the body, leaving the remainder colorless. These lines of pigment appeared strikingly amoeboid in their movements, changing quite rapidly during the time required for a camera sketch. The same change took place in the first individual before cytolysis occurred.

DIMENSIONS.—Length, 106–115$\mu$; transdiameter, 51–63$\mu$; diameter of nucleus, 16–18$\mu$.

OCCURRENCE.—This species was first taken 2 miles off La Jolla, California, on July 3, 1906, with a No. 20 silk net in a haul from 155 meters to the surface. Two individuals were taken July 16, 1917, in a surface haul at the end of the pier at the Biological Station at La Jolla in a surface temperature of 21.5 C.

ACTIVITIES.—One individual moved slowly without rotation in anticlockwise circles about twice the length of the body in diameter. The movements of the pigment, prior to cytolysis, in streams along the girdle and sulcus and in the longitudinal lines coincident with or parallel to the longitudinal striae is suggestive of an intimate relationship between locomotor organs and the metabolic processes concerned in the formation and distribution of pigment.

COMPARISONS.—This species is close to *Pouchetia juno* Schütt in size, median location, and horizontal axis of the ocellus as well as in its structure. The differences lie in the striae of *P. violescens*, which are not recorded for *P. juno*, which has, moreover, peripheral ringlike platysomes not present in *P. violescens*. These are superficial characters, easily overlooked and possibly, in the case of platysomes, evanescent. The structure of the girdle and sulcus, however, is different in the two species. The anterior flagellar pore in *P. juno* is 0.3 of the total length from the anterior end, while in *P. violescens* it is 0.45 with a corresponding increase in the length and torsion of the apical loop of the sulcus.

*P. violescens* is a typical member of the subgenus *Pouchetiella* and with *P. polyphemus* and *P. juno* forms a group of large species with median ocellus. A similar group of large species in the subgenus *Pouchetia sensu strictu* includes *P. maxima, P. voracis,* and *P. fusus,* in all of which the lens is lobed or subdivided.

*P. violescens* is the only violet species thus far known among the Gymnodinioidae. Pale glaucous bluish colors are rather common and a darker blue is known in *Gymnodinium coeruleum*. It is also the only species in *Pouchetia* which is noticeably striate, the nearest approach to striations appearing in *P. maxima* and *P. striata*.

## **Pouchetia voracis** sp. nov.

Plate 8, figure 89; text figure PP, 2

DIAGNOSIS.—Large species with rotund body, its length 1.3 transdiameters; girdle with 1.25 turns around body, displaced 0.4 total length; sulcus with torsion of 0.5 turn; ocellus concentrated, median; lens elongated, lobed; pigment mass with black, amoeboid melanosome with red central core; core, spinel red. Length, 68μ. Pacific off La Jolla, California, July, August.

DESCRIPTION.—The body is large, rotund, broadly ovoidal in contour, with the epicone and hypocone subequal. The epicone presents a large, hemispherical apex. Its length is 0.3 above the anterior flagellar pore and at its distal extremity, 0.8 of the total length of the body. The measurements of the hypocone are somewhat smaller, being anteriorly 0.7 and posteriorly 0.2

of the total length of the body in length. The antapex is rounded, asymmetrical, longer upon the right side, the deep channel of the distal end of the sulcus forming a broad trough, deeply furrowing its left ventral face and slightly notching the antapical margin.

The junction of the girdle and the sulcus occurs at a distance of 0.3 of the total length of the body from the apex. Thence the furrow sweeps around the body in a uniformly descending left spiral of 1.25 turns as a broad, rather deep trough, its width being 0.07 transdiameter. In an individual which had devoured a thecate *Peridinium* (fig. PP, 2) the girdle is distorted so that it steepens rapidly in the proximal half to 50° from the horizontal, flattens again almost to the horizontal middorsally, and then descends gently at 20° to its posterior junction with the sulcus. This occurs at 0.25 of the total length from the antapex. The sulcus takes origin at or very near the apex. It sweeps 0.25 turn around the epicone to its anterior junction with the girdle. It forms a deep trough in its posterior course, with a total torsion of 0.5 turn of a descending left spiral, and widens below its distal junction with the girdle to twice its width above. Below the junction it curves across the hypocone to the antapex, notching its postmargin slightly. The lips of both girdle and sulcus form prominent, slightly overhanging ridges, especially anteriorly. The anterior flagellar pore is found at the proximal junction of the girdle and sulcus, the posterior one slightly beyond its distal junction. The transverse flagellum traverses about 0.5 the entire length of the girdle.

The ocellus is of the concentrated type and is situated in a midventral position on the left side of the sulcus. Its length is 0.45 to 0.60 transdiameter and its main axis is horizontal and directed ventrally in one individual (pl. 8, fig. 89) and vertically with an anterior direction in another (fig. PP, 2). The direction of both is probably affected by the presence of adjacent food bodies. The lens is of the concentrated type, elongated, smooth or slightly lobed in outline, where crowded upon a food mass (fig. PP, 2) of a dull, opaline-green color, and showing faintly outlined concentric layers. The base is more or less deeply imbedded in the large, amoeboid melanosome which at times almost covers it, then retreats, leaving it exposed for nearly its entire length. The central core is large and scarlet red to maroon in color. A few large granules of black or red pigment are found in the peripheral cytoplasm near the girdle.

The nucleus is large, ellipsoidal, and located in the anterosinistral region. Its major and minor axes are 0.65 and 0.5 transdiameter in length respectively. Distinct parallel, crowded, chromatin strands pass obliquely across its main axis.

A small, club-shaped pusule opens into the anterior and another into the posterior flagellar pore, each with its apex directed towards the equatorial plane.

*Pouchetia voracis,* like many of the Gymnodiniidae, is a voracious feeder. In one individual (fig. PP, 2) the still connected but collapsed theca of a large *Peridinium,* resembling *P. crassipes,* was found crowded into the posterosinistral region, and pushing the ocellus against the sulcus. The contents had apparently been digested, leaving only the shell, the plates of which were becoming displaced, as though by pressure. These plates still preserved many of their characteristic markings, as if unaffected by the digestive processes. The whole mass was enclosed in a large food vacuole. Along the ventral side of the body were a row of blue-green peripheral rodlets, all at right angles, or nearly so, to the surface. These rodlets were not present in the other individuals figured (pl. 8, fig. 89), and are evidently correlated with the metabolism ensuing upon digestion. In a second individual small food masses, one ochraceous, were crowded between nucleus and ocellus. The cytoplasm is clear and very finely granular with a few oil drops centrally located. There were no peripheral vacuoles present.

The color, which is a clear spinel red, is concentrated in a thin peripheral layer, immediately underneath the periplast, leaving the inner protoplasm quite clear. In some cases the border of the girdle shows a narrow, blue-green line.

A large, thin, hyaline cyst enclosed the individual figured, inside of which was a second, smaller one of the same appearance. These were both ellipsoidal in form and more widely detached anteriorly and ventrally than posteriorly and dorsally. The second individual was

also encysted and had external thickenings of the cyst wall about the apex above the apical loop of the sulcus and along the girdle, indicating greater secretory activity anteriorly and along the motor region.

DIMENSIONS.—Length, 68–80μ; transdiameter, 50–67μ; major and minor axes of nucleus, 37–42μ and 20–25μ; ocellus, major axis, 21–26μ.

OCCURRENCE.—The first specimen was taken from a haul made on July 27, 1917, 4 miles off La Jolla, California, with a No. 25 silk net from a depth of 80 meters to the surface, in a surface temperature of 21°9 C. Another from a haul August 17, 0.75 mile off La Jolla, at a depth of 80 meters to the surface, in a surface temperature of about 22° C.

ACTIVITIES.—One individual was kept under observation from 2 P.M. to 3 P.M., when cytolysis ensued. It was encysted and inactive, but when the slide was tapped it rotated a few turns within the cyst. When rolled over by moving the cover glass it always returned to the same position as though passively by gravity.

Unimpeachable evidence of the holozoic nutrition of this species is presented by the remains of the component plates of the theca of a large *Peridinium* within a food vacuole of an encysted individual of this species. Its contents had been almost completely digested. The manner in which a *Pouchetia*, with an almost labile protoplasmic body, devoid of protrusible food-grasping organs, can capture, hold, and engulf a *Peridinium*, more than half its size, passes comprehension. From the location of the *Peridinium* in the body of its captor it seems probable that it was taken in through the sulcus below the anterior flagellar pore and the posterior end of the body, that is, mainly through the intercingular sulcus. A mobility of this region sufficient to capture a mobile *Peridinium* and ingest its rotund body with protruding apical and antapical regions requires an efficiency of function quite beyond that suggested by the structure of these regions of *Pouchetia*, and exceeds, to a high degree, our preconceptions as to the instincts, reactions, and capacities of these unicellular organisms.

COMPARISONS.—This is one of the least specialized species of the subgenus *Pouchetiella* with concentrated ocellus. Its lens, when in juxtaposition with a food mass, is slightly lobed, its melanosome is irregular if not slightly lobed, and detached globules of red or black pigment are found near the girdle. The integration of lens and pigment is well established, but the position of the ocellus is shifted by the pressure of food masses.

*Pouchetia voracis* is close to *P. striata*, but is less rotund, more asymmetrical posteriorly, has a shorter apical sulcus, and proximal epicone with less torsion, and less intercingular displacement of the girdle. The ocellus has a slightly more anterior position and similar structure, but is less distinctly laminate. It also lacks entirely the longitudinal striations characteristic of *P. striata*.

CHAPTER XX

# POUCHETIIDAE (*continued*): PROTERYTHROPSIS, ERYTHROPSIS SUMMARY

## **PROTERYTHROPSIS** gen. nov.

Text figure PP, 9

Diagnosis.—Pouchetiidae with median girdle, posterior ocellus, stout rudimentary tentacle or prodlike antapical process, with no paracingular lines and no recess about the base of the prod. Type species *Proterythropsis crassicaudata* sp. nov.

### Discussion

This genus includes only a single species whose structure is such that it is excluded on the one hand from *Pouchetia* and on the other hand from *Erythropsis*. It is a typical *Pouchetia* in all features except in the presence of the posterior prod. The presence of longitudinal rows of pigment granules is also somewhat unique for *Pouchetia*, within which the linear organization of the peripheral plasma in any fashion is rarely evident, appearing as striae only in *P. striata*, *P. maxima*, and *P. violescens* and as pigment granules with the merest trace of linear arrangement in *P. maculata*. In the one species known in *Proterythropsis* there is a well defined but locally restricted expression of this linear organization in the arrangement of the peripheral spherules of pigment.

It is excluded from *Pouchetia*, however, by the presence of a posterior prod not unlike those of *Erythropsis*, except in size, slight development, and absence of a recess about its base. It is excluded from *Erythropsis*, however, not only by this lack but also by the arrangement of girdle and sulcus, which is quite typical of that in *Pouchetia*, and also by the entire absence of anything suggestive of the paracingular lines which parallel the girdle. In view then of the absence of the recess, flattened epicone with apical horn, and paracingular lines, it is impossible to include the species in *Erythropsis*. In view of the fact that it affords a transition in structure looking towards the genus *Erythropsis* from the types evolved in *Pouchetia*, the new genus *Proterythropsis* has been established to receive it. The nature of its most characteristic structure, the posteroventral prod, is unfortunately not well established or fully described owing to the mobility of the organ and of the organism carrying it. In so far as position, direction, morphological relations, and activities are concerned, it appears to be the same organ as the prod of *Erythropsis*, only in an initial stage of evolution.

Its primitive or generalized stage is indicated by the absence of recess, of terminal stylet, lack of development of circular and longitudinal contractile fibers, the protractor and retractor muscles, and of a capitate end. The ventroposterior direction is perhaps less advanced than the posterior direction seen in all species of *Erythropsis* except *E. protrudens*, in which the direction of the prod is the same as in *Proterythropsis*.

That we have in this genus a connecting link between *Pouchetia* and *Erythropsis* is further supported by the fact that the posterior end of *Pouchetia*, in some species with the antapical loop of the sulcus twisted about that part of the hypocone below the distal end of the girdle, is highly mobile in life, and, as we have observed in several such species, somewhat protrusible, though it never forms a permanent prod. In this connection it is well to recall the fact that the prod of *Erythropsis* is subject to remarkable changes in shape and extension.

The nucleus, with moniliform chromatin threads, is of the *Pouchetia* type, rather than that of *Erythropsis*, which is remarkably clear in life and often has a perinuclear clear zone.

Only one species, the type, *Proterythropsis crassicaudata*, is known in this genus.

### **Proterythropsis crassicaudata** sp. nov.

Plate 11, figure 123; text figure PP, 9

Diagnosis.—A medium sized species, ellipsoidal, length 1.4 transdiameters; girdle a descending left spiral of 1.2 turns, displaced 0.8 transdiameter; sulcus of 0.3 turn; ocellus of distributed type, posterior, with elongate segmented lens and reddish-black pigment mass and red central core; stout tentacle-like ventroposterior process. Length, 70μ. Pacific off La Jolla, California, July.

Description.—The body is asymmetrically ovoidal, widest just below the anterior posteroventral receding face; the outline broken by a tentacle-like process projecting ventroposteriorly. The epicone equals the hypocone in length but exceeds it considerably in volume. It is broad, hemispherical at the apex, with a length above the anterior flagellar pore of 0.25 and from its distal extremity of 0.7 the total length of the body. The hypocone bulges out ventrally below the proximal end of the girdle, is deeply grooved above the sulcus and the whole ventral face recedes posterodorsally about 25° from the vertical. The antapex is then pushed dorsally. It is asymmetrically hemispheroidal, without sulcal notch.

The girdle meets the sulcus anteriorly at a point 0.25 of the total length of the body from the apex. It sweeps around the body in a descending left spiral of 1.2 turns before joining the sulcus again at a point 0.18 of the total length of the body from the antapex. Its total displacement is thus 0.57 of the total length. It lies in a broad, deep trough, the margins of which bulge outward in high ridges. Its width is 0.08 transdiameter, its anterior lip overhangs, and it is deeply impressed. The anterior flagellar pore is located at the anterior junction of girdle and sulcus and the posterior one at the distal junction. The transverse flagellum traverses only 0.2 of its total length, probably foreshortened as cytolysis approaches. The stout longitudinal flagellum may be coiled about the prod.

The sulcus invades the epicone but a short distance beyond the anterior flagellar pore as a shallow trough. Below this point it descends posteriorly as a slender channel in a deep trough, whose borders form high ridges on either side. Beyond the distal junction of the girdle and sulcus it traverses the hypocone but a short distance as a shallow channel. Its total torsion is only 0.3 turn, but the apical section may be incompletely delineated.

The ocellus is located in the ventral region close to the posterior flagellar pore and to the left of the sulcus. Its length is 0.5 transdiameter and it is directed anteroventrally about 45° from the vertical. The lens is oblong, somewhat claviform, and is composed of four unequal, hyaline, colorless spheroidal or ellipsoidal moieties, closely pressed together in a linear series decreasing in size towards the melanosome. Its base is imbedded in the amoeboid pigment mass. The greater part of this is rose red in color, with a smaller mass of black pigment on the ventral side. The central core is red.

The nucleus is large, ovoidal, and anteriorly placed in the ventral part of the epicone. Chromatin strands follow the course of its major axis. Its major and minor axes are 0.8 and 0.4 transdiameter respectively in length.

A large club-shaped pusule opens anteriorly into its anterior flagellar pore. The posterior one was not observed. The cytoplasm is rather coarsely granular and clear with a few large, bluish vacuoles in the anterior region. Two dark olive buff food bodies were present posteriorly. On the dorsal side of the body, peripherally located, are many rufous colored granules, gathered near the girdle and extending anteriorly in longitudinal rows, about eight in number, in the peripheral plasma to near the apex. Rod-shaped masses of the same rufous material are found along the proximal border of the girdle in the posterior region. On the opposite side from the ocellus are several subparallel rows of granules and several larger spherules of the same rufous material. No surface markings or striations were present.

The color is a light, dull yellow mixed with grey and distributed quite uniformly through the cytoplasm.

The most remarkable organ of this animal is the contractile prod which emerges from the widened sulcus just below the distal end of the girdle and hangs pendant ventroposteriorly at about 45° from the horizontal in its basal part, then curves posteriorly. In form it is a curved cone with rounded apex. Its length and basal diameters are 0.50 and 0.24 transdiameter respectively and the angle of the core is approximately 25° when the prod is extended. When contracted it merges somewhat basally with the ventral face of the hypocone. The recession of the ventral face of the hypocone is apparently correlated with the development of this protrusion and the consequent withdrawal of the material from this region utilized in its formation. The cavity about the base is so slight as not to merit the designation of a recess such as occurs in *Erythropsis*.

Dimensions.—Length, 70$\mu$; transdiameter, 49$\mu$; axes of nucleus, 29$\mu$ and 19$\mu$; length of ocellus, 20$\mu$; length of fully extended prod, 25$\mu$.

Occurrence.—A single individual was taken July 25, 1917, 11 miles off La Jolla, California, with a No. 25 silk net in a haul from 80 meters to the surface, in a surface temperature of 21°7 C.

Activities.—The animal progresses by rotation and circling in anticlockwise spirals several times its length in diameter and when quiescent the prod is seen to undergo somewhat spasmodic contractions. They are not repeated as regularly and rapidly, nor are its excursions so extended as in *Erythropsis*.

Comparisons.—The median location and the displacement of the girdle are not unlike that seen in *Pouchetia striata* and *P. voracis*, and the structure of the ocellus is quite similar to that of *P. maculata*, although the pigment has less

melanin. The torsion of the body, as shown by the course of the sulcus, is only 0.2 turn, far less than in any species of *Pouchetia*, and thus more like that of *Erythropsis* The stout longitudinal flagellum recalls that figured by Schütt (1895) for *Pouchetia cornuta* (=*Erythropsis cornuta*).

## **ERYTHROPSIS** Hertwig

Plate 12, text figures RR–VV

"Acineten" Metchnikoff (1872), pp. 7–9; (1885), p. 433.
*Erythropsis* Hertwig (1884), pp. 204–212, pl. 6.
*Spastostyla,* Vogt (1885*a*), in part, p. 53; (1885*b*), pp. 183–187, fig. 1.
*Pouchetia,* Schütt (1895), in part, pl. 26, figs. 95, 96.
*Erythropsis,* Delage and Hèrouard (1904), pp. 387–388, figs. 680, 681.

### Diagnosis

Gymnodinioidae with flattened epicone less than 0.25 the size of the hypocone, flattened anteriorly and with or without a small curved apical horn. Ocellus very large, composed of one or several hyaline lenses attached to or

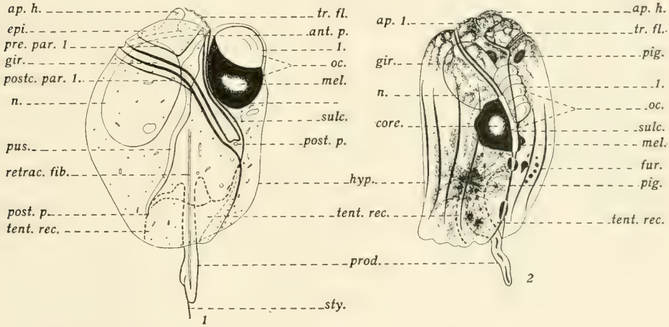


Fig. RR. 1. *Erythropsis cornuta* (Schütt). 2. *E. scarlatina* sp. nov. Abbreviations: *ant. p.*, antapical pore; *ap. h.*, apical horn; *ap. l.*, apical loop; *core*, core of melanosome; *epi.*, epicone; *fur.*, furrow; *gir.*, girdle; *hyp.*, hypocone; *l.*, lens; *mel.*, melanosome; *n.*, nucleus; *o.*, ocellus; *pig.*, pigment; *post. p.*, posterior pore; *post. par. l.*, postcingular paradinial lines; *pre. par. l.*, precingular paradinial lines; *prod*, prod or tentacle; *pus.*, pusule; *retrac. fib.*, retractor fibrillae; *sulc.*, sulcus; *sty.*, stylet; *tent. rec.*, recess of prod or tentacle; *tr. fl.*, transverse flagellum. × 500.

imbedded in the side of a red, brownish or black pigment body with a red, brown, or yellow core, located to the left of the intercingular sulcus. The girdle makes a single, descending sinistral turn and may be bordered by the precingular and postcingular grooves which we designate as the paracingular grooves or lines. The sulcus expands posteriorly into a ventroposterior tentacular recess from the center of which springs a posteroventrally or posteriorly

directed tentacle or prod which in several species attains a length twice that of the body and is subject to incessant rhythmical contractions. It may or may not have a capitate end and a terminal stylet. An attachment area may be found at the distal end of the girdle. The form is somewhat rigid and the surface almost differentiated into a distinct pellicle, mottled by vacuoles as cytolysis approaches. No striae are present. Anterior pusule attached to the anterior flagellar pore and another to the tentacular recess. Posterior longitudinal flagellum probably present in addition to tentacle, but evanescent or easily lost. A single ellipsoidal nucleus present. The chromatin network not distinct in life. Perinuclear zone with vacuoles and envelope are sometimes present. No chromatophores. Pigment usually confined to the ocellus, distributed as a network of scarlet in one species. Plasma homogenous and translucent. Nutrition evidently holozoic. Binary fission not observed. Autotomy of tentacle and cytolysis occur on slight stimulus.

All small, marine species 48–130$\mu$ in length. Ten species known from warm temperate and tropical seas.

### Description

The form of the body in *Erythropsis* is highly specialized, due to the invasion of the hypocone by the ventral recess (fig. RR, *tent. rec.*), the foreshortening of the epicone, and its apical flattening. This form appears to have been brought about by a reversion from a condition of greater torsion, so that the sulcus, instead of having a considerable obliquity in the intercingular area, as in *Pouchetia*, has, in *Erythropsis*, an almost straight course in this section, and the distal end of the girdle in compensation is deflected abruptly posteriorly in the distal 0.15 or so of its course. The result of this reduction in torsion is apparent in the almost horizontal course of most of the girdle, its marked distal deflection, and the straight intercingular sulcus. Accompanying these modifications of the girdle and sulcus, and possibly the prime cause of their origin, is the considerable increase in relative size of the ocellus and its anterior location. The ventral recess is a deep excavation opening ventroposteriorly and sheltering the basal end of the prod. Ventrally it is the continuation of the sulcus and posteriorly it is terminal and even axial. It also contains the opening of the posterior pusule, the posterior flagellar pore, and the posterior flagellum. It is thus the deeply recessed posterior end of the sulcus.

The ocellus of *Erythropsis* is in all cases premedian, often far anterior, usually protuberant, directed anteriorly, never horizontally or posteriorly. It is also relatively very much larger than in *Pouchetia*. It is present in both the diffuse type (subgenus *Polyopsidella*) and the integrated subgenus *Erythropsis*. The integrated forms attain a high degree of specialization, as in *E. cornuta*, *E. protrudens*, and *E. pavillardi*. It is a matter of note, as indicating that the whole organism shares this specialization, that it is in these same species that the paracingular lines and the prod are also highly developed. The presence

of a pigmented sensory core is a prominent feature in the integrated type of ocellus. The structural and morphological evidence is strong that the ocellus of *Erythropsis* is functionally the most efficient optical organ among the Dinoflagellata and the Protozoa as a whole.

The "tentacle" (Hertwig, 1884), or dart ("dard," Fauré-Fremiet, 1914), or prod as we designate it (fig. RR, *prod*), is located ventrally in *E. extrudens* or ventroposteriorly in *E. minor* and *E. scarlatina*, and posteriorly and axially in the remaining species. It may be capitate, as in *E. labrum*, *E. pavillardi*, and *E. extrudens,* or lack distal enlargement as in the other species. It may have a terminal stylet, as in *E. hispida, E. extrudens,* and *E. cornuta*, or lack this, as in other species. It has an axial, longitudinal, contractile group of fibers, the retractor fibrillae (fig. RR, *retrac. fib.*), and a series of circular ones, the protractors. These antagonistic groups give to the organ an extraordinary degree of mobility and render possible the extension of this organ to a length four times that of the body. The operation of a Lamarckian factor of activity of this organ in the origin of the ventral recess about its base and in the pushing of the ocellus far anterior is suggested by the structural features of the genus. One who has watched this organ in action has its potency strongly intimated to him.

The occasional persistence of the longitudinal flagellum alongside this organ precludes any possibility that it is a modified posterior longitudinal flagellum. It appears rather to be a mobile margin of the sulcus specialized as an axial organ, as foreshadowed in the prod of *Proterythropsis* and the mobile antapex of *Pouchetia* and *Cochlodinium*.

The paracingular lines which border the girdle on both sides in *E. cornuta*, *E. richardi, E. labrum,* and *E. extrudens* (fig. RR, *pre. par. l., post. par. l.*), and may have been wholly or in part overlooked in the other species, are faint modifications of the surface pellicle, or even slight modifications of the contours which run parallel to the margins of the girdle throughout its whole course. Their functional significance is wholly obscure and their homology quite problematical. The nearest approach to anything like them in the Dinoflagellata are the precingular and postcingular series of plates in the thecate forms. But there can be no possibility of the origin of such rows of plates from these paracingular areas. The similarity of the relationship of the paracingular lines on the one hand and the rows of plates on the other to the girdle suggests the function of the latter in influencing, if not originating, such organs.

The presence of huge melanosomes and of the red pigment in the plasma of *E. scarlatina* and in the sensory core of the ocellus of most species, and in the entire pigment mass of *E. agilis*, establishes the predominance of the red end of the spectral colors in this genus, thus continuing the same relationship of these pigment colors to specialization which was detected in the genus *Pouchetia*.

No chromatophores are present. No food balls have been detected, but it is probable that the species are holozoic, as is *Pouchetia*.

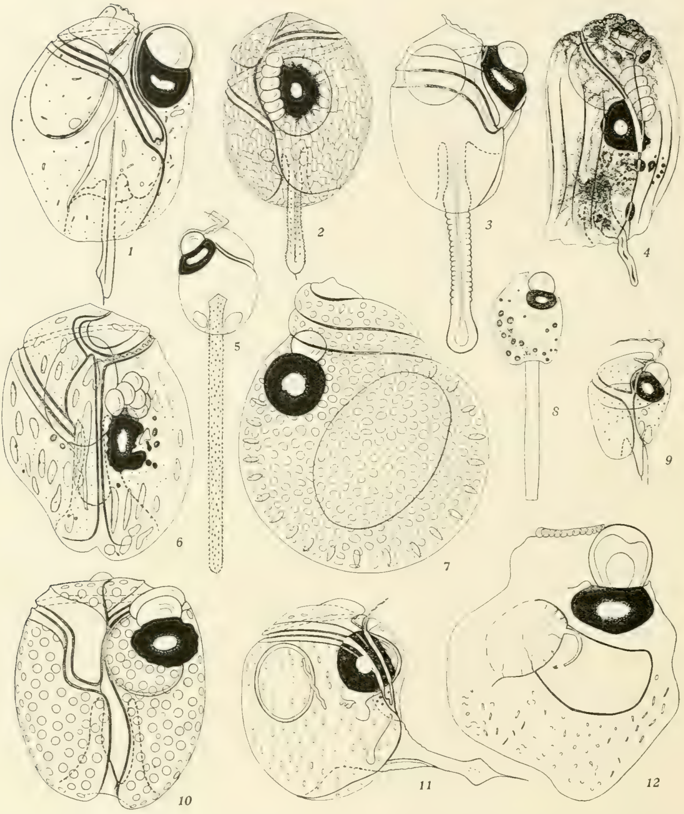


Fig. SS. *Erythropsis* Hertwig. Magnification 500, unless otherwise stated. 1. *E. cornuta* (Schütt). Ventral view. 2. *E. hispida* sp. nov. Ventral view. 3. *E. pavillardi* nom. sp. nov. Left side. 4. *E. scarlatina* sp. nov. Ventral view. 5. *E. pavillardi* nom. sp. nov. Right side. After Pavillard (1905, pl. 3, fig. 1). 6. *E. labrum* sp. nov. Ventral view. 7. *E. cochlea* (Schütt). Dorsal view. After Schütt (1895, pl. 26, fig. 95). 8. *E. agilis* Hertwig (1884, pl. 6, fig. 8). Ventral view. × 250, approximately. Girdles and sulcus not shown in original figure. 9. *E. minor* sp. nov., ventral view. 10. *E. richardi* sp. nov. Ventral view. 11. *E. extrudens* sp. nov. Right side. 12. *E. agilis* Hertwig. Ventral view. After Hertwig (1884, pl. 6, fig. 1). Magnification approximated from statement of lenses used.

The genus *Erythropsis* is the most highly specialized of all the Gymnodinioidae as shown in accessory paracingular grooves along the girdle, the apical horn, the ocellus, and the complete integration of its constituent lens and pigment mass and in the prod with its functional specialization. The ocellus and prod alike attain a degree of structural complexity and diversity in the genus unequaled among all of the Protozoa. As an organ adapted in structure to the performance of specific function the ocellus is of the same order of magnitude, though not of dimensions and cellular components, as the ocelli of the Hydromedusae, Turbellaria, and Rotifera, and the tentacle or prod is in like manner structurally comparable to those of the simpler Hydroida, though not their equivalent in function. The organization of the living substance into organs for bodily functions is evidently, in the light of these extraordinary structures of this unicellular organism, not a *function of the number of nuclei*, but rather of *the organism as a whole*. The cell theory as a basis of organization breaks down when we attempt to apply it to the organs of the Protozoa.

## Distribution

The species of *Erythropsis* thus far discovered have all been found in warm temperate to subtropical oceanic seas under strikingly similar conditions. The eight species discovered at San Diego, in the summer of 1917, were all taken within a period of three weeks and at the same locality. In some instances several species were taken in the same five-inch net. We have found no evidence of either seasonal or geographical isolation of these species. The possibility of a vertical stratification within the eighty meters traversed by our collecting nets is, however, not excluded by our data, but seems highly improbable.

## Historical Discussion

The history of this remarkable genus is as complicated as its own extraordinary combination of organs, and involves one of the most instructive controversies in the history of the biological sciences in the past century. It illustrates, on the one hand, the value of the scientific caution of the original describer, and, on the other, the recklessness of his critic and the resulting depth of error into which his unbridled zeal for exposure carries him when, without having seen the object under discussion, he ventures to discredit the work of another.

The genus was described by Professor Richard Hertwig (1884), who found a single individual in the plankton of the Mediterranean at Sorrento, Italy, in the Easter vacation. Upon placing it under the cover glass for examination it dropped off its tentacle, whereupon it was at once fixed in osmic acid and stained and mounted. Professor Hertwig's account of this remarkable organism was therefore based upon his recollection of a brief glimpse of the active animal under a low magnification and a closer study of its mutilated and somewhat distorted remains. His conclusions, as to the relationship of this bizarre animal, were that it was undoubtedly a protozoan and one of the Infusoria, although

he noted that, in the possession of an eyespot composed of a pigment mass and a lens, and in the presence of a highly contractile "tentacle," the degree of organization presented by the organism was unusual for the Protozoa. Hertwig (1884) did not attempt to determine the relationships of his *Erythropsis*, but suggested that it was near the Infusoria and that its cuticula, nucleus, and opercular apparaus allied it to the vorticellid, but that the characterisic cilia of these ciliates had not been observed in his new genus. He makes no suggestion of any relation of *Erythropsis* to the Dinoflagellata, though he does cite *Leptodiscus* and *Noctiluca* in discussing the question of its degree of specialization.

Shortly after the appearance of this cautiously worded account of this weird protozoan by the young docent at Bonn the veteran zoologist, Carl Vogt, of Geneva, attacked (1885*a*) with characteristic vigor the validity of Hertwig's interpretation. He requested his colleagues to debar *Erythropsis* from the "catalogue" of animals and stated dogmatically that it was "in der That" only a detached vorticellid, *Spastostyla sertulariarum* Entz, which had had the misfortune to have been thrown into osmic acid by the Bonn zoologist just as it was in the act of swallowing a marginal eyespot of a half rotten medusa, probably *Lizzia*.

Hertwig (1885) published a reply to this attack upon his interpretation stating his grounds for believing that *Erythropsis* was a real organism and not the monstrous aggregation which Vogt had interpreted it to be. Vogt, however, returned to the attack (1885*b*) in a caustic article entitled "Ein wissenschaftlicher Irrthum," published in the widely distributed *Die Natur*, a popular scientific journal, in which he made clear his duty to expose the error, the grounds upon which the exposure rested, and controverted Hertwig's reply, treating him anonymously. "Der Mensch irrt, so lange er lebt," writes Vogt, and then proceeds to distinguish, as particularly harmful to science, those errors in fact, such as false accounts of organisms which cumber synonymy, and give rise to unsupported hypothesis.

Ein neuer Organismus wird beschrieben, dessen ganzer Bau, wenn er wirklich existirte, unsere Begriffe von der thierischen Zelle, von den einzelligen Urthieren mit Allem, was drum und dran hängt, gänzlich über den Haufen werfen würde. Was ist zu thun? Schweigt man still, so zieht die unerwartete Thatsache stets weitere und weitere Kreise. Die jüngeren Forscher, meist wenig zur Kritik geneigt und dem Worte des Meisters treu, machen aus dem neuen Steine die Grundlage ihrer Spekulationen und theoretischen Gebäude; es eröffnen sich groszartige Perspektiven; man sieht schon weitere Verzweigungen und Anknüpfungen der jetzt so beliebten Stammbäume, die ohne Rücksicht auf Zeit und Raum zusammen geflickt werden, wie die Stammbäume der Paladine, die alle von flüchtigen trojanischen Helden ausgingen. So gibt man sich, neben den vergeblichen Nachforschungen um weitere Exemplare des so hoch interessanten und merkwürdigen Thieres, viel Mühe, Noth und Plage, bis endlich die Seifenblase platzt, welche dem Ganzen zu Grunde lag.

He then descends to doggerel:

> Was man in Osmium besitzt,
> Kann man bequem nach Hause tragen!
> Und wenn man d'ran gezeichnet und geschwitzt,
> Auch manches Schöne d'rüber sagen.

and erects the deadly parallel column in the form of comparative figures of "*Erythrypsis agilis;* nach R. Hertwig" and "*Spastostyla sertulariarun;* nach Geza Entz."

The impartial observer's estimate of the fairness of the critic's attack must be influenced by the fact that the figure of *Erythropsis agilis* which Vogt states is "nach R. Hertwig" is not a reproduction of any of Hertwig's (1884) figures, but is a highly modified combination of Hertwig's figures 2 and 8. The modifications are: (1) the elongation, curvature, and narrowing down of the nucleus in the direction of the vorticellid type of nucleus; (2) the change of the continuous spiral (as Hertwig had drawn it) into an adoral zone of separated membranelles, as a sheath containing a fibrillar axis as in *Vorticella* instead of a homogeneous solid cylinder as distinctly figured by Hertwig.

With this deadly parallel before his readers, Vogt proceeds to demonstrate that, part for part, Hertwig's *Erythropsis* is nothing but a *Vorticella,* its tentacle being the stalk of the ciliate while the eye is that of a medusa lodged in the gullet of the *Vorticella* fixed at the instant of swallowing. To add poignancy to the thrusts of his criticisms he further illuminates the enormity of the error by publishing "nach den Brüdern Hertwig" figures of the ocelli of *Lizzia* and *Nausithoe,* whose similarity to the pigment spot and lens of *Erythropsis,* as Vogt figures them, is little less than damning.

In extenuation of Vogt's conclusions it is to be noted that the dimensions, which may be approximated from the recorded systems of objectives and oculars used in making the figures of *Erythropsis,* and the ocellus of *Lizzia,* are such that such a combination of eyespot and *Vorticella* is spatially possible, and furthermore that Hertwig's figures (1878, pl. 8, figs. 9, 10) of the ocellus of *Lizzia* and that of the lens and pigment mass of *Erythropsis* have much in common in appearance, though structurally entirely different, as Hertwig (1885) had shown. Hertwig's figure (1884, pl. 6, fig. 7) of the pigment arranged in striate radial fragments about the lens of *Erythropsis* as shown in side view is remotely like his figure of the ocellus of *Lizzia* (1878, pl. 8, fig. 9) in face view with radially arranged striate pigment masses encircling the lens. It should also be noted that Hertwig (1884) compares the tentacle with the stalk of *Vorticella* in that it is homogeneous, and has a fine cuticula.

In treating of Hertwig's reply and reaffirmation that there are no cilia upon *Erythropsis,* Vogt (1885*b*) merely condemns the certainty of the reaffirmation and compares it with the cautious statement regarding cilia not having been observed, in the previously published account. He concludes that the

defense has but served to confirm his conviction that his exposure of Hertwig's error is sound, and that *Erythropsis* is only a *Spastostyla* which had been killed in the act of eating the ocellus of a medusa.

Some months after Vogt's exposure, Metchnikoff (1885) published a brief note stating that he had seen an organism, which resembled that described by Hertwig, in the living material taken in the tow net off Madeira, and had made a brief reference to it in 1874 in a short note in Russian concerning his "Reise nach Madeira." He suggested its affinities to the suctorian *Ophryodendron*.

Thereafter *Erythropsis* disappeared from zoological literature, as Vogt (1885) had advised, for nearly a score of years. It does not appear in Bütschli's (1881–89) monograph of the *Protozoa*, or in any of the monographic treatises or text books written since Hertwig's paper was published, with the single exception noted below. Nor did Schütt, either in his monograph (1896) of the Peridiniales or in his Plankton Expedition report (1895) make any mention of Hertwig's discovery. This is perhaps not strange since no one had as yet suggested its affinities to the Dinoflagellata, and no investigator of this group or subsequent observer had as yet seen any species of the new genus or verified Hertwig's discovery. Pouchet (1884, 1885*a*, *b*, 1886*a*, *b*, 1887) had in a series of papers called attention to the ocellate Dinoflagellata but overlooked Hertwig's related *Erythropsis*. It was still under the cloud of suspicion raised by Vogt's criticisms, so that its true relationship was as yet unsuspected. The latter is probably the case with Schütt's omission, since he describes, as *Pouchetia cochlea* and *P. cornuta*, two organisms which exhibit unmistakable resemblances to *Erythropsis*. They both lacked "tentacles." However, this is a condition frequently observed, in our experience, in other species of *Erythropsis* in which the tentacle or prod is often dropped off prior to cytolysis.

The genus remained in this neglected condition until 1896, when Delage and Hèrouard in the course of their reorganization of the genera of the Protozoa in their *Traité de Zoologie Concrète* brought this genus into relation with the Dinoflagellata. They were still cautious, however, and admitted it only in an appendix to this group, stating: "Il nous semble qu'il y a une autre manière de voir plus vraisemblable que les précédentes et que nous hasarderons tant elle nous semble probable, mais sous toutes réserves et sans réconnaître le danger qu'il y a à formuler une opinion sur un être que l'on n'a pu examiner."

It was not until 1904 that Pavillard (1905), himself an investigator of the Dinoflagellata, found at Cette on the Mediterranean a single individual which he recognized as an *Erythropsis*. He had a brief opportunity to sketch the animal and concluded that it was Hertwig's species rediscovered. He also for the first time accorded it unquestioned place with the affiliated genera *Pouchetia* and *Gymnodinium;* but, owing to the paucity of his material, he did not recognize that his species was distinct from that of Hertwig, and that Schütt (1895) had previously seen two other species of the genus, but, not recognizing *Erythropsis* as a dinoflagellate, had placed these species in *Pouchetia*.

The species was next discovered by Collin (1912), who recorded the discovery of another individual in the student laboratory at Cette; also Fauré-Fremiet (1914) stated that Chatton had seen one at Banyuls-sur Mer, in the Mediterranean. Thus up to the time of Fauré-Fremiet's discovery of his "vingtaine" of individuals at Croisic on the west coast of France only six individuals had ever been recorded, and observations on these had been restricted because of the rapidity of cytolysis.

Unfortunately the misunderstandings which in the past had accumulated about *Erythropsis* were not dissipated by Fauré-Fremiet's more abundant material. He regards his species as identical with Hertwig's *E. agilis*. It has, however, a brown instead of a red pigment mass, albeit with a prominent red core. Its proportions and structure, especially the ocellus, are so similar to those of *Erythropsis* figured by Pavillard (1905) from Cette that we regard it as *E. pavillardi* nom. sp. nov, and not *E. agilis* Hertwig.

In three other very important particulars Fauré-Fremiet (1914) brought confusion with regard to this slightly known organism. In the first place, he oriented it with the epicone posterior and the prod anterior, thus reversing the previous orientation. He also described and figured the transverse flagellum as arising in the distal end of the girdle from the attachment area, and running around the body in the reverse of the direction universal in the Dinoflagellata. Lastly he figures the longitudinal flagellum as emerging anteriorly from the epicone. We have elsewhere (see Kofoid and Swezy, 1917) given the grounds upon which these three conclusions should be rejected as wholly untenable.

## Species and Distribution

The first record of any form now referable to *Erythropsis* was made by the eminent Russian biologist Metchnikoff, who published (1874) in his account (in Russian) of his "Riese nach Madeira" a brief account of a delicate and evanescent infusorian from the collections of the tow net in the tropical Atlantic off Madeira in 1872, but did not figure or name it. He later (1885) recognized its similarity to Hertwig's *Erythropsis agilis*, but believed its affinities to be with the Suctoria.

This genus now includes ten species. The first of these is *Erythropsis agilis*, the type species originally described by Hertwig (1884) from the vernal plankton of the Mediterranean off Sorrento. *E. cochlea* and *E. cornuta* were figured by Schütt (1895) as *Pouchetia cochlea* and *P. cornuta* from the collections of the Plankton Expedition, presumably from the tropical Atlantic or from the Bay of Naples. These, as figured, lack the prod, but the ocellus and epicone are typically those of *Erythropsis*. In 1905 Pavillard described and figured a small species taken from the Mediterranean at Cette in October as *E. agilis* Hertwig. This was about half the size of Hertwig's form with a girdle located farther posteriorly, especially towards its distal end and with a black instead of a red pigment body. In view of the speciation recorded by us in this genus and the significance of size, girdle, and pigment mass in specific distinctions

therein, it seems imperative to conclude that Pavillard's (1905) form is not that of Hertwig (1884), but a distinct species which we call *Erythropsis pavillardi* nom. sp. nov. In addition to these four species, *E. agilis, E. cochlea, E. cornuta* (Schütt), and *E. pavillardi*, previously occurring in the literature, we have brought to light six new species from the plankton of the Pacific off La Jolla, California, to wit: *Erythropsis extrudens* sp. nov., *E. richardi* sp. nov., *E. hispida* sp. nov., *E. labrum* sp. nov., *E. minor* sp. nov., and *E. scarlatina* sp. nov.

It has not been possible, in the brief time and with the often scanty material available for the inspection of the new species here described, to determine all of the structural details essential for an adequate description. The locomotor activities and the ceaseless rapid contractions of the prod preclude continuous close observation while the normal structure persists, and cytolysis abruptly terminates all possibility of further examination when activity ceases. Discrepancies and inconsistencies with regard to such structures as the longitudinal flagellum, the attachment area, and incomplete delineation of the complicated contour and furrows of the epicone are attributable to these baffling difficulties.

The prod or tentacle itself is subject to great modification in shape, position, and completeness during the period of observation. All of our figures have of necessity been made from individuals which have slowed down. In these the prod is foreshortened by contraction, and perhaps in some cases has even undergone autotomy. It was not infrequently entirely lacking in some individuals under observation, as it is in Schütt's (1895) figures of *Pouchetia cochlea* and *P. cornuta*. While it is by no means certain that it is normally present in both of these species of Schütt, the fact that we have found it present in all species we have figured, including *Erythropsis cornuta* (Schütt), though not in all individuals of these species which we have had under observation, leads us to infer that it is a normal organ in the genus *Erythropsis*, and will ultimately be found in *E. cochlea* Schütt also. In view of these considerations we have included Schütt's (1895) *Pouchetia cochlea* in *Erythropsis*, although no prod appears on his figures.

It is obvious from an inspection of the comparative figures (see text fig. SS) of the known species in the genus *Erythropsis* that they fall into two groups, those with diffuse or compound lenses and lobed or radiate pigment masses, referable to the subgenus *Polyopsidella* and the subgenus *Erythropsis sensu strictu*, with condensed or simple undivided lens and compact pigment mass. This first group exhibits the principle of repetition of parts and might be cited as expressing multiple similar factors. Some degree of correlation between lens and pigment spot appears in the fact that subdivision of the lens is in every case accompanied by radiations (*E. hispida*) or lobing (*E. labrum*) of the pigment mass, though not by its complete subdivision. On the other hand, the remaining seven species of the genus have an undivided lens and a compact pigment mass without trace of lobes.

### 1. Subgenus **Erythropsis** (Hertwig)

Ocellus with single lens and undivided or non-lobed pigment mass, crowded upon the left margin of the sulcus and protuberant anterolaterally. Type species *E. agilis* Hertwig. Includes also *E. cochlea* (Schütt), *E. cornuta* (Schütt), *E. pavillardi* nom. sp. nov., *E. extrudens* sp. nov., and *E. minor* sp. nov.

### 2. Subgenus **Polyopsidella** subgen. nov.

Ocellus with several lenses superposed, in a linear series, or closely grouped, pigment mass lobed, radiate or scattered. Type species, *E. scarlatina* sp. nov. Includes also *E. hispida* sp. nov., *E. labrum* sp. nov., and *E. richardi* sp. nov.

### Key to the Species of **Erythropsis**

1. Ocellus with single subhemispherical lens ........ 2
1. Ocellus with a compound lens of several distinct elements ........ 3
2. Tentacle directed posteriorly ........ 4
2. Tentacle directed obliquely ventral, capitate, with terminal stylet ........**extrudens** sp. nov.
4. Pigment of ocellus bright red ........**agilis** Hertwig
4. Pigment of ocellus black or nearly so ........ 5
5. Lens subhemispherical, pigment mass spheroidal, nearly twice diameter of lens, hypocone subcircular in lateral outline ........**cochlea** (Schütt)
5. Lens more nearly hemispherical, less than 1.5 diameter of the lens, hypocone elongated .... 6
6. Epicone with distinct horn curved towards the left ........ 7
6. Epicone without horn, hypocone tapering, tentacle tapering, with stylet ......**minor** sp. nov.
7. Tentacle slender, asymmetrically capitate, with stylet ........**cornuta** (Schütt)
7. Tentacle long and stout, without stylet ........**pavillardi** nom. sp. nov.
3. Body pervaded anteriorly and ventrally with scarlet pigment, ocellus with a row of five lenses ........**scarlatina** sp. nov.
3. Body without scarlet pigment ........ 8
8. Lens composed of numerous small rounded elements ........ 9
8. Lens composed of two large, superposed elements ........**richardi** sp. nov.
9. Lens composed of a line of five flattened ellipsoids, pigment brownish ........**hispida** sp. nov.
9. Lens composed of a cluster of about seven spheroids, pigment black ........**labrum** sp. nov.

### **Erythropsis agilis** Hertwig

Text figures SS, 8, 12

(?) "Acinetea," Metchnikoff (1874), pp. 7–9.
*Erythropsis agilis* Hertwig (1884), pp. 204–212, pl. 6, figs. 1–10; (1885), pp. 108–112.
*Spastostyla sertulariarum,* Vogt (1885*a*), p. 53; (1885*b*), pp. 183–187, fig. 1.
*Erythropsis agilis,* Metchnikoff (1885), pp. 433–434.
*E. agilis,* Delage and Hèrouard (1896), pp. 387–388, figs. 680, 681.
*E. agilis,* Pavillard (1905), pp. 48–49, pl. 3, fig. 1 (= *E. pavillardi* nom. sp. nov.).
*E. hertwigi,* Jollos (1910), p. 203. *Lapsus* for *E. agilis* Hertwig.
*E. agilis,* Poche (1913), p. 162.
*E. agilis,* Fauré-Fremiet (1914*c*), in part, pp. 27–47, text figs. 2 A–C. Pl. 1 and text figs. 1, 3–12 are *E. pavillardi.*
*E. agilis,* Kofoid and Swezy (1917), pp. 89–102, text figs. 9, 10.

Diagnosis.—A large species with rotund body, truncate posteriorly; its length 1.4 transdiameters; epicone flattened, small apical horn present; ocellus simple, protuberant; lens spherical, with red flattened hemispherical pigment mass; extended prod four times length of body. Length of body about 100$\mu$. Mediterranean off Sorrento, April.

Description.—Hertwig's (1884) figures and account of this species are the basis of this description written from our present knowledge of the structure of the genus, which enables us to interpret his data more completely. The body is rotund, wider posteriorly, its extreme length in life, excluding prod, 1.4 transdiameters. The anterior part is flattened dorsoventrally and expanded laterally, the widest part being slightly posterior to the equator. The dorsoventral diameter is 0.99 of the transverse. The epicone is low and flattened anteriorly, its length is 0.2 of the total length. There appears to be a slight anterior horn, an elevation probably encircled by an apical spiral which is evidently the anterior extension of the sulcus upon the epicone. In Hertwig's figures (1884, pl. 6, figs. 3, 5) of this spiral it passes at the *right* side of the horn and thence around to the left, not the reverse, as in our figures of this region in other species. The hypocone forms at least 0.9 of the body, is almost circular in cross-section in the equatorial region, flattened somewhat ventrally, truncated posteriorly and is cleft to the center by the deep slitlike tentacular recess.

The girdle is not clearly or consistently figured. It may begin anterior to the ocellus and terminate near the problematical tentacle-like structure figured by Hertwig in the right mid-ventral region. If so, its displacement is about 0.35 transdiameter, and the spiral crown on the anterior margin of Hertwig's figure must be in the rear, not the front of the body, and the central spiral loop on the epicone of his figure must be the amoeboid upper end of the anterior spiral of the sulcus, and not any part of the girdle or transverse flagellum. There are suggestions in the contours of Hertwig's figures of paracingular lines and bands, but they are not defined in either text or figures. The sulcus likewise is not indicated at all in his view of the ventral surface sketched from memory of the living form. The tentacular recess is clearly defined only in the one view (see his fig. 3) from the posterior end. It cleaves the body to the center, but no indication of its anterior limits in the body in life or in the preserved individual are available. The prod, as figured and described, is a cylindrical truncated structure twice the length of the body when contracted and four times its length when expanded. Neither granulations on the surface nor terminal stylet were noted, and no axial fiber, although Vogt (1885*b*, fig. 1) reproduces Hertwig's figure with such an axis to demonstrate its similarity to the stalk of a vorticellid. Hertwig (1884) does, however, note the presence of folds on the prod at disintegration, presumably the lines of constriction of the circular fibers.

The ocellus is located opposite the region of the intercingular part of the sulcus. It is of the simple type with a spherical lens with concentric laminae and a flattened hemispherical, red-pigment mass. Its total length is about 0.35 the total length or 0.45 transdiameter and its axis is deflected to the left and ventrally about 5° from the major axis. The diameter of the lens is a little over 0.25 transdiameter and it is sunk into the pigment mass for about one-third of its diameter. It is made up of five concentric laminae, the outermost of which contains a lens-shaped thickening on its axial, anteriorly directed region. The pigment mass is a reddish, flattened hemisphere, 1.35 times the diameter of the lens in diameter on its posterior face, and a low truncated cone anteriorly into which the lens fits. In the stained and mounted specimen the pigment mass shows radial striations and cleaves along these lines. No central core was noted.

The nucleus is an ellipsoidal body, 0.6 transdiameter in length, flattened on the ventral face (by shrinkage?) and located near the center of the body. It has a chromatin reticulum but not moniliform threads. Numerous reddish-brown granules are scattered in the peripheral plasma, especially posteriorly.

A peculiar organ, designated by Hertwig (1884) as a "spoon" or spear, is figured at a point corresponding to the right side of the sulcus, near its junction with the distal end of the girdle and possibly the upper end of the tentacular recess. It is a recurved ectoplasmic structure. Its significance is problematical. It might be the contracted longitudinal flagellum, or the denuded axial fiber of the tentacle or possibly an artifact. Its location militates against the first two suggestions. Hertwig (1884) does not figure a longitudinal flagellum.

DIMENSIONS.—These are computed on the basis of Hertwig's (1885) statement that the organism is 120$\mu$ in length. Length, 120$\mu$; transdiameter of body, 84$\mu$; diameter of lens, 32$\mu$; of pigment body, 45$\mu$.

OCCURRENCE.—One individual seen by Professor Richard Hertwig in April, 1884, in the plankton of the Mediterranean off Sorrento, Italy.

ACTIVITIES.—The tentacle was exceedingly active, contracting to half its fully extended length, which was four times that of the body. The tentacle was dropped off when the animal was placed under the cover glass.

SYNONYMY.—This is the type species of the genus and of the new subgenus *Erythropsis sensu strictu.* There is no critical evidence that the assignment by Metchnikoff (1874) of the organism he discovered off the Madeira Islands in 1872 to *E. agilis* is correct. In so far as his brief description goes, it might equally well be applied to several other species in the genus. It will suffice to regard it as an *Erythropsis* and questionably *E. agilis* Hertwig.

Pavillard's (1905) assignment of a single individual discovered by him at Cette to this species must be set aside and this individual assigned to a new species, *E. pavillardi*, on grounds given elsewhere in this paper. Jollos (1910) inadvertently uses the name *Erythropsis hertwigi* in referring to the organism discovered by Hertwig. This name has no valid status.

It seems probable that the species described by Fauré-Fremiet (1914) as *E. agilis* Hertwig is in reality *E. pavillardi* nom. sp. nov. We have elsewhere discussed (see Kofoid and Swezy, 1917) the grounds upon which we reject Fauré-Fremiet's proposed orientation of *Erythropsis "agilis"* with the tentacle or prod anterior.

COMPARISONS.—This species is one of the specialized forms of the genus with concentrated ocellus and large and powerful tentacle. Its ocellus resembles that of *E. pavillardi* and *E. minor*, but it is much larger than either of these species and has an entirely different tentacle, neither capitate nor tapering and without stylet. Hertwig's (1885) statement, if correct, that the length is 120$\mu$ makes *E. agilis* next to the largest species in the genus. It is exceeded only by *E. cochlea.*

### **Erythropsis cochlea** (Schütt)

Text figure SS, 7

*Pouchetia cochlea* Schütt (1895), pp. 96, 169, pl. 26, fig. 95.

DIAGNOSIS.—A very large species with rotund body, its length 1.2 transdiameters; girdle displacement (?); ocellus not protuberant, with small spheroidal lens, and a large black spheroidal pigment mass; prod not noted; peripheral vacuoles subpolygonal, crowded. Length, 130$\mu$. Atlantic (?) or Bay of Naples.

DESCRIPTION.—Owing to the fact that Schütt (1895) gives only a single figure, of the dorsal side, with very incomplete delineation of girdle and little of the sulcus, our description is limited. However, an analysis of this figure in the light of the fuller knowledge of the genus is desirable for the orientation of the species.

The body is very rotund, its length 1.2 transdiameters. Epicone 0.25 of the total length, culminating at the left in a blunt apical point, sloping to the right about 20° and ventrally. The hypocone has almost a circular outline to the level of the girdle, above which the epicone is abruptly reduced, especially at the right, to 0.6 the greatest diameter, which is 0.4 of the total length from the antapex. The right side is more rotund than the left and the antapex is hemispherical.

The girdle is not differentiated in form in Schütt's figure from the precingular and post-cingular grooves. Assuming that the apical point is encircled by the upper end of the sulcus, it appears that Schütt has represented below this trough of the sulcus the precingular groove and the girdle below it. It forms a descending left spiral of considerable displacement. The furrow, as figured, is no more than a narrow groove. The sulcus is entirely without representation, except for the uppermost part, as above interpreted. No indication of tentacular recess or of the prod is given. The precingular groove is well defined, parallel to the girdle and separated from it at all points on the dorsal side by a distance of 0.11 transdiameter. The surface between the girdle and the precingular groove is convex.

The ocellus is composed of a spheroidal lens of concentric layers, 0.16 transdiameter in diameter, imbedded in the anterior face of a spherical pigment mass 0.23 transdiameter in diameter. It is black peripherally with a reddish-brown core. These are like scattered pigment granules or processes.

The nucleus (?), as figured by Schütt, is extraordinarily large. It is ellipsoidal in form with its major axis 0.72 and its minor axis 0.48 transdiameter in length. It lies obliquely across the right side of the hypocone. The surface of the body is closely set with compressed sub-polygonal uniform vacuoles, about forty across the dorsal side at the equator. In optical section a radially arranged group of structures of about twice the size of the superficial vacuoles is figured in the peripheral cytoplasm of the hypocone. They do not appear to be rhabdosomes, nor are they in size and distribution the equivalents of the superficial vacuoles above noted.

DIMENSIONS.—Length, 130$\mu$; transdiameter, 110$\mu$; diameter of lens, 17$\mu$; of pigment mass, 27$\mu$; of nucleus, 75$\mu$.

OCCURRENCE.—Figured by Schütt (1895) from the Bay of Naples or the Atlantic. We have not found it at San Diego.

COMPARISONS.—Schütt's figure suggests an *Erythropsis* in a moribund condition, as indicated by the rounded form, the contracted state of the transverse furrow, and by the vacuolated periphery. The absence of the extended prod is confirmatory evidence of this supposition. The ellipsoidal structure in the hypocone which we have tentatively interpreted as the nucleus may be a food body. The fact that the nucleus is extraordinarily transparent in *Erythropsis*, and usually lies far anterior, while in Schütt's figure this ellipsoidal structure is far posterior, gives rise to this alternative interpretation. This is the largest species known in the genus, the most rotund (as figured) and has the concentrated form of ocellus resembling that of *E. cornuta*, *E. minor*, and *E. extrudens*.

The structure of the epicone with its anterior horn or apical point with encircling anterior loop of the sulcus and its precingular groove are entirely typical of *Erythropsis*, and not of *Pouchetia*, and the ocellus is of the simple

type found in one group of species in *Erythropsis*, but not in *Pouchetia*. For this reason we include this species in *Erythropsis*. It is a highly specialized form, as well as the largest.

### Erythropsis cornuta (Schütt)

Plate 12, figure 129; text figures RR, 1; SS, 1; UU

*Pouchetia cornuta* Schütt (1895), pl. 26, figs. $96_{1-3}$.
*P. cornuta*, Lemmermann (1899), p. 360.
*P. cornuta*, Lang (1901), p. 161, fig. 75 A.
*P. cornuta*, Pavillard (1905), p. 48, as synonym of *Erythropsis agilis* Hertwig.

Diagnosis.—A large species with ovoidal body; length 1.25 transdiameters, with distinct curved apical horn; girdle displaced 0.65 transdiameter; ocellus protuberant; lens simple, hemispherical; pigment mass subhemispherical, with red core; prod capitate, with terminal stylet, axially located. Length, 104μ. Atlantic, Pacific, off La Jolla, California, July, August.

Description.—The body is ovoidal, widest anteriorly, its length 1.25 transdiameters, dorsoventral and transdiameters equal. The epicone is small, its diameter in ventral view less than 0.5 transdiameter, apex broadly rounded with a short but very clearly differentiated hook-shaped apical horn about two widths of the girdle in height and curved to the left. Ventrally the height of the epicone is only 0.25 transdiameter, except in the slender, posterior projection along the distal end of the girdle which reaches a little beyond the middle of the body. The epicone contains less than 0.15 of the total volume of the body. The hypocone has a length midventrally of 0.75 of the total length of the body and much more dorsally. Its anterior region is contracted to about 0.5 transdiameter to meet the small epicone. Its right side is more convex, its left somewhat flattened below the ocellus, and the body contracts gradually posteriorly to 0.4 transdiameter at its somewhat truncate antapex.

The girdle originates at the anterior flagellar pore above the ocellus, forms a flat spiral slightly below the anterior margin on the left and dorsal sides, and in the distal quadrant turns posteriorly at an angle of about 30° from the horizontal, increasing to 70° in its most distal region to its junction with the sulcus. The total displacement in the intercingular region is 0.65 transdiameter. The transverse flagellum reaches about 0.5 of the circumference. The furrow is sharply but not deeply impressed and is bordered by parallel paradinial lines. The anterior paracingular band is wider than the posterior, the former slightly exceeding, the latter slightly less than the width of the furrow. These lines are clearly defined in this species. At the distal end of the furrow on its anterior margin is a deep pit, the attachment area, the point at which presumably the anterior horn of the posterior schizont remained jointed to the anterior sister cell at binary fission. The sulcus is a very narrow groove running from the anterior flagellar pore obliquely posteriorly on the right side of the ocellus, curving again below it to the left and continuing beyond the middle of the body to its junction with the tentacular recess. This cavity is broadly and asymmetrically campanulate, with a dorsal ledge, a deep pit around the shaft of the prod and a wide right flap which projects over the midventral region. The depth of the recess is 0.3 of the total length of the body. No longitudinal flagellum was seen, but the posterior pusule may mark the point of its origin.

The prod is elongate cylindrical, reaching, when extended, a total length 2.3 that of the body, and when fully contracted retreating wholly within the postmargin of the tentacular recess. It is distinctly capitate distally, with a knob twice the diameter of the shaft at the

maximum of contraction and about 1.5 diameters when extended. Long before cytolysis sets in the size of this knob was reduced by a distal sloughing off of its substance which first became limpid clear and then detached itself with adjacent granular plasma. Both before and after this sloughing it was distally somewhat asymmetrical. There is a small articular, distal stylet whose length does not exceed the diameter of the shaft and a central axial retractor fibril, but no marked evidence of circular protractors.

The ocellus is relatively small. Its length is 0.42 transdiameter and its major axis is deflected about 25° to the left and ventrally from the axis of the body. It projects from the body almost the full length of the lens. The lens is hemispherical, consists of regular, equidistant, concentric laminae and is buried slightly in the black melanosome of the pigment mass. This is subhemispherical, being enlarged on its lower outer region. It contains a coral-red core.

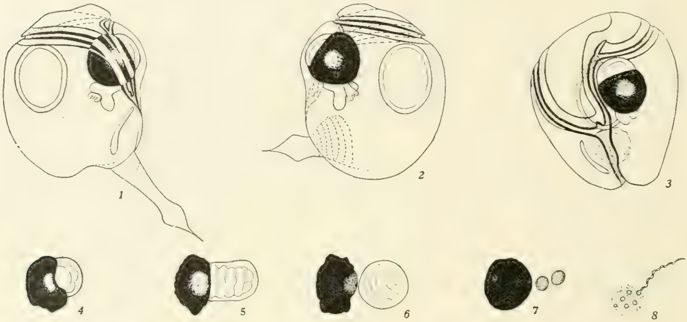


Fig. TT. *Erythropsis extrudens* sp. nov. 1. View of the right side with tentacle fully extended. 2. Left side, tentacle retracted. 3. Anteroventral view of moribund individual showing granular stump of amputated tentacle and structure of epicone with girdle and paradinial lines. 4. Ocellus shortly before cytolysis, showing modifications of concentric lines in the lens. 5. Ocellus shortly after cytolysis of cell body, showing zone of solution about the distended lens. 6. Rounding up of detached lens, red core still in melanosome. 7. Last stages of solution of melanosome and core. 8. Persistent transverse flagellum after cytolysis. × 333.

The nucleus is ellipsoidal, with major and minor axes of 0.57 and 0.40 transdiameters respectively. It lies obliquely in the right anterior part of the body. The chromatin network was not visible. The anterior pusule arises at the anterior flagellar pore, passes posteriorly obliquely across the level of the girdle, where it expands somewhat and is continued obliquely posteriorly to an opening at the right side of the tentacular chamber, at a point which may correspond to the posterior flagellar pore. The two pusules are thus in this individual connected in a continuous canal. Several refractive oil granules lie in the plasma adjacent to the sulcus, and a small food remnant lies near the nucleus. Peripheral vacuoles of circular to linear form and minute size filled with a bluish-green fluid lie in the peripheral plasma. The general color tone of the plasma is a pearl grey.

Dimensions.—Total length, 104$\mu$; of extended tentacle, 240$\mu$; of ocellus, 33$\mu$; transdiameter, 81$\mu$; diameters of nucleus, 42$\mu$ and 34$\mu$.

Occurrence.—Three individuals taken in collections made with a net of No. 25 silk from a depth of 80 meters, 6, 4, and 0.75 miles off La Jolla, California,

July 23 and 27 and August 20, 1917, in surface temperatures of about 20°2 C, 21°4 C, and 22° C.

Schütt (1895) figures it, presumably from the Bay of Naples or from the Atlantic.

ACTIVITIES.—The individual under observation was brought to the laboratory at 10 A.M. and was first captured in the large jar of fresh sea water at 4 P.M. and placed under the cover glass. It remained active for only a few moments, keeping the prod in rapid, regular contractions several times per second and moving spasmodically in an anticlockwise circle of short radius. The prod soon began to slough off, its contractions to become irregular, and the outward thrust to grow shorter and shorter, until within an hour all movement ceased and cytolysis ensued.

SYNONYMY.—Figured as *Pouchetia cornuta* by Schütt (1896, pl. 26, figs. $96_{1,2}$), who failed to recognize its relationship to Hertwig's *Erythropsis*. The fact that he does not list Hertwig's (1884) paper in his bibliography or recognize the genus in his *Pflanzenfamilien* (1896) indicates that he did not recognize *Erythropsis* as a dinoflagellate. His figure and text alike show that he did not recognize the tentacle or prod. His drawing was evidently made from a moribund specimen.

COMPARISONS.—Our individual appears to be identical with the form figured by Schütt (1895, pl. 26, fig. 96) as *Pouchetia cornuta*. His magnification gives a length of 105μ for his smaller figure and 120μ for the larger, at the same magnification. However, the magnification is not given for the larger figure, though both are said to have been made from the same living cell. The tentacle is probably represented by the rounded knob from whose base the longitudinal flagellum springs. The outline, girdle, sulcus, and paracingular lines are strikingly similar in his figures and ours, although he did not record the intercingular part of the sulcus, and undoubtedly portrays incorrectly the proximal end of the girdle as ascending to the tip of the apical horn. This horn is also figured as deflected to the right, whereas we record it as deflected to the left. This may be due to its mobility or to inaccuracy of record on the part of one of us. In view of the difficulties in securing an accurate interpretation of this obscure region, these discrepancies may be regarded as negligible, in so far as they affect the question of specific identity.

This species is close to *E. agilis* Hertwig, but differs in shape of the body and lack of broadly truncate antapex. The ocellus is of the same simple type, but the melanosome is extended longitudinally instead of transversely, as in *E. agilis,* and the apical horn is more fully developed. The body is smaller and far less rotund than in *E. cochlea* (Schütt) and larger and stouter than in *E. pavillardi*, and its prod is of a different type, having a terminal stylet. The posterior position of the prod differentiates it from *E. extrudens*, and its very large size and long prod, as well as its much deflected, distal end of the girdle, separate it from *E. minor*.

## **Erythropsis extrudens** sp. nov.

Plate 12, figure 130; text figures SS, 11; TT

DIAGNOSIS.—A large species with rotund body, flattened anteriorly, slightly laterally compressed posteriorly; epicone at left forming 0.2 total length; hypocone deeply furrowed ventrally by tentacular recess; girdle displaced posteriorly about 0.5 total length; stout oblique contractile prod or tentacle with capitate-pointed end, terminating in a stylet; ocellus slightly protuberant with concentric hemispheroidal lens, black pigment, and red core. Length, 89$\mu$. Pacific, off La Jolla, California, July.

DESCRIPTION.—The body is rotund, collapsed posteriorly in individuals which have dropped off their tentacle, spheroidal in active forms with tentacle intact. The anterior end is much flattened and the posterior notched by the deep sulcus and tentacular recess. In collapsed individuals the posterior end is laterally compressed to about 0.5 transdiameter anteriorly.

The body is so diversified by the girdle and its attendant paracingular grooves, the protruding eyespot, the deep sulcus, and the basal mass of the tentacle that the unraveling of its complicated structure is a matter of serious difficulty, especially since the animal while intact is incessantly on the jump, so that complete camera outlines are impossible and the views presented change with every move of the animal. The analysis here given is the result of the prolonged study of three different individuals, only the first of which possessed this tentacle, the mutilated base alone remaining on the other two.

The greatest difficulty attends the analysis of the girdle and sulcus, because of their routes on the flattened apex and across the black pigment mass, and because of the paracingular grooves which confuse the observer. The analysis made on the three individuals is sufficiently coherent to lend support to the hope that it is the correct one, but the difficulties are so baffling that certainty has not been attained.

The girdle is of the *Gyrodinium* type, that is, displaced at its distal end posteriorly for a considerable distance, about 0.5 of the total length of the body. The flagellar pore of the transverse flagellum lies in a depression just anterior to the ocellus. From this point the girdle sweeps dorsally around the flattened epicone under a widely overhanging upper lip and descends rapidly as a relatively shallow furrow, obliquely posteriorly across the right face, terminating at a posteriorly directed notch on the edge of the deeply infolded, ventral sulcus. The very active transverse flagellum traverses the proximal 0.6 of this girdle.

The sulcus invades the epicone for a short distance above the anterior flagellar pore, skirts the right side of the ocellus, sinks deep into the tentacular recess which is continued posteriorly across the antapex. No longitudinal flagellum could be found. Its point of origin, or the posterior flagellar pore, may be located at the opening of the posterior pusule. The notch at the distal end of the girdle was not detected on the individual with the tentacle while it was active. This is probably the attachment area.

The epicone thus has a length on the left side of the sulcus of about 0.2 and on the right side of about 0.66 of the total length of the body, but owing to the rapid descent of the girdle in its distalmost part the epicone as a whole forms but a small part (less than 0.1) of the total body.

The girdle is attended, in fact paralleled throughout most of its course, by certain surface depressions, or paracingular grooves or lines (fig. RR, *post.* and *pre. par. l.*) strongly suggestive at first sight of the slightly impressed, spirally twisted sulcus of *Pouchetia* and *Cochlodinium*. Repeated efforts to bring these shallow markings into agreement with such an interpretation and to give to the furrows the organization of *Pouchetia* which the presence of the eyespot leads one to expect were fruitless. Semiapical views of collapsed and therefore quiet individuals

finally gave the clue to the interpretation here presented. Paralleling the furrow of the transverse flagellum throughout most, if not the whole, of its course, both anterior and posterior to it, are shallow depressions—the paracingular grooves. The anterior, or precingular, groove is the more plainly visible, more deeply impressed, and is separated by a somewhat wider interval from the furrow than the postcingular groove, except where the latter skirts the right side of the sulcus.

The most remarkable feature in the structure of this bizarre animal is its ventral tentacle or prod, a mobile and rhythmically contractile structure, located towards the posterior end of the body in the midventral plane in the tentacular recess of the expanded sulcus. It is an elongated structure, consisting of a base, shaft, head, and stylet, extending ventroposteriorly in the median plane. It is held habitually in this plane at an angle of 10°–25° below the horizontal. It is, however, capable of a considerable latitude of movement (fig. TT, 1, 2) and exhibits much flexibility in action. It rises from a low, spreading, convex, granular base, which is 2.5 times the thickness of its shaft in diameter, and extends for 0.5 its length in a rounded mass into the elsewhere hyaline substance of the body. The exposed conical portion forms an asymmetrical cone of about 40°, which forms about 0.33 of the length of the partially extended tentacle, or almost wholly disappears in the fully extended one (pl. 12, fig. 130). When the prod is fully contracted this base swells up into a rounded dome which now includes most of the substance of the cylindrical shaft. This shaft is the connecting link between the head and the base and emerges at the expense of the substance of the latter. When fully extended it is cylindrical throughout, about 0.6 the diameter of the head in diameter and 0.8 of the length of the body in length. The head is subsymmetrically biconical, 0.15 of the length of the body in diameter, and its proximal and distal conical surfaces subtend angles of about 60° and 70° respectively. Distally it passes abruptly into a rodlike stylet, 1.25 its diameter in length. This is a cylindrical hyaline rod, not a mobile flagellum, although it has some elasticity, bending when in contact with the substrate, but having no independent motion of its own.

From the right side of the base of this prod there passes distally on its surface in a partially spiral course a shallow, granular line, possibly a groove. This terminates on the outer face of the head. The only plausible explanation of this is that it is the morphological extension of the sulcus. Owing to the folded contour of the sulcus at the base of the tentacle, nothing more than the union of this groove at its proximal end with the sulcus could be detected. It is to be noted that this point of juncture is immediately adjacent to the notch of the distal end of the girdle and not far from the possible location of the flagellar pore.

The internal structure of this remarkable organ consists merely of a light area, a vacuole in the head, and two sets of antagonistic striations, outer circular and inner longitudinal, marked by lighter lines and attendant granulations in the case of the circular fibers. Their behavior in the contracted and extended condition of the tentacle indicates their function as protractor and retractor muscles.

The second outstanding feature of this species is the eyespot or ocellus. It consists of three parts, the lens, melanophore or melanosome, and core, the latter two constituting the pigment mass. It is located far anteriorly, immediately posterior to the proximal end of the girdle in the projecting lobe formed by the anterior angle of the hypocone to the left of the intercingular sulcus. It lies beneath a rounded eminence more evident in an obliquely lateral view of the right side of the body. The lens is directed anteroventrally and is elongate hemispherical in form with its base buried in the pigment mass. It consists of three concentric masses of hyaline material, the middle one of which is internally trilobed, and the outermost shows minor concentric lines. It is not externally lobed or divided. On cytolysis it elongates and shows a semisegmented form with a clear membrane and then rounds up in a spheroidal lump (text fig. TT, 4–7).

The pigment mass consists of a black melanosome surrounding and almost hiding a bright red central core and changes outline with the varying positions of the body and with the approach of cytolysis. It varies from flattened to elongate hemispherical form with varying irregularities on its surface, but had no amoeboid, dendritic or reticulate processes when observed. Several detached globules of the pigment lie on either side of the girdle just below the ocellus.

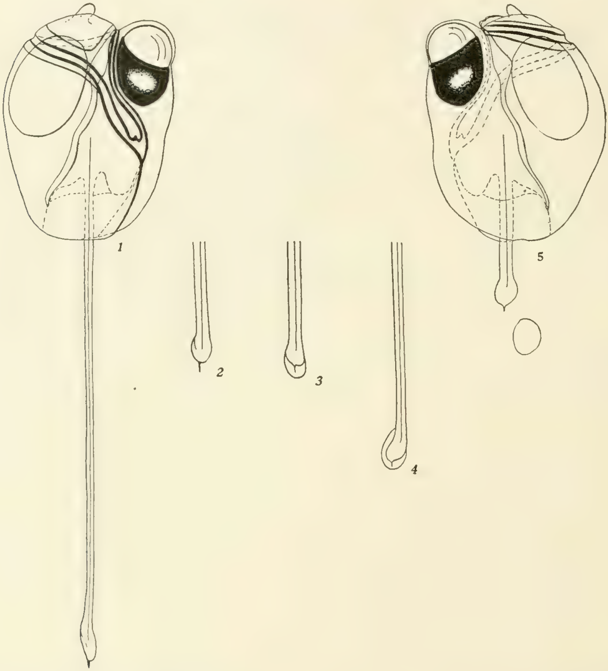


Fig. UU. *Erythropsis cornuta* (Schütt). 1. Ventral view with prod fully expanded. 2–4. Stages in sloughing off end of prod. 5. Dorsal view with tentacle partly retracted. Blob below cast off plasma from prod. × 500.

There is a large sacklike, clear, pinkish pusule extending posteriorly from the anterior flagellar pore on the dextrodorsal side of the ocellus and another smaller pink sack with lobed diverticula, posterior to the ocellus and adjacent to the distal end of the girdle. The connection of this with the pore by a canal was not noted. The anterior sack was far less pink in color than is usual with the contents of pusules. It seems probable, but not certain, that these two structures are pusules attached respectively to the anterior and posterior flagellar pores.

The nucleus is a very clear, broadly ellipsoidal body in the anterodorsal region, with major and minor axes of 0.5 and 0.4 transdiameter respectively. It has an outer clear zone enclosed within the outer nuclear membrane. No chromatin strands could be detected in its substance. The cytoplasm of the body as a whole was throughout of a glassy, glaucous, hyaline appearance with remarkably few alveoli or granules of appreciable size.

The surface of the body is devoid of striae or other markings except for the lines and zones paralleling the girdle. However, as the animal grows less active, peripheral vacuoles arrange themselves in the subsurface zone in a somewhat linear fashion, with their longer axes longitudinal and their lines longitudinally disposed, indicating at least an internal linear organization of the peripheral layer of cytoplasm.

DIMENSIONS.—Length of body, 90–117$\mu$; of extended tentacle, including stylet, 60–70$\mu$; of stylet, 17$\mu$; diameters, transverse 70–85$\mu$, dorsoventral 73$\mu$.

ACTIVITIES.—Only one normally active individual has been under observation. This was swimming rapidly in anticlockwise spirals of a radius not exceeding several lengths of the body, without rotation except for an occasional somersault. During this period, and subsequently when the circus motions slowed down, the prod was incessantly repeating its rhythmical contractions with brief intermissions.

After about thirty minutes under the cover glass the contractions slackened in vigor and slowed down from the earlier rate of 80 per minute, became less regular, and of smaller amplitude, and finally ceased. Shortly after this the contracted prod was detached at its base by local cytolysis and speedily disintegrated, with only a few circular and longitudinal fibers remaining intact for a brief time.

The behavior of this strange organ was observed for about two hours before it was cast off and underwent immediate cytolysis. When first observed the animal was very active, swimming about in anticlockwise spirals. When the spiral circling ceased temporarily the tentacle still kept up a continuous, rhythmical, alternating retraction and protraction without cessation or modification, except as interfered with by the substrate or other obstacles, or by the locomotor activities of the animal. When first timed, at a stage of somewhat slackened activity, these recurrent thrusts of the prod were carried on at the rate of one every 0.75 second. The regularity of the action was remarkable and the continuity of it equally impressive and no less exasperating when one was attempting to get a sketch, to say nothing of a camera outline, of this extraordinary animal.

The action was continued whether in contact with the substrate or not. In case the extending tentacle met the resistance of another body this was vigorously thrust away if it was a small one. If, on the other hand, it was larger, as in the case of the carapace of a copepod, the body of the *Erythropsis* was itself pushed away at once by the vigorous thrust of the prod. The terminal stylet exhibits considerable rigidity under such impacts. The result when the prod met the substrate was equally effective. When lying obliquely on its side the tip of the prod was in contact with the glass and this contact was sufficient

continuously to thrust the body backward for a distance equal to 0.25 to 0.50 its diameter with each thrust of the prod.

Cytolysis of the body ensued about an hour after autotomy and disappearance of the prod. The approach of this catastrophe is first indicated by the rapid formation of minute liquid spherules extruded simultaneously on all sides of the body, apparently by the discharge of the fluid accumulating in the peripheral vacuoles. This is speedily followed by the rupture of the peripheral pellicle, the outpouring of the contents of the body and its rapid and complete liquefaction. The reversal of the living substance from a gel to a sol is complete and takes place with remarkable rapidity, the pellicle disappearing as rapidly as the cell contents (text fig. TT, 8). In the last vestiges of the granular cytoplasm the short transverse flagellum was observed with active undulating contractions still passing through it. The organs which resist solution longest are the nucleus and the ocellus. The nucleus gradually wastes away, the peripheral clear zone and chromatin network becoming more distinct before final disruption and solution. It appears to be a more resistant gel than the surrounding cytoplasm.

The cytolysis of the ocellus (figs. TT, 4–7) when released by solution of the surrounding cytoplasm proceeds slowly to a complete disappearance in about twenty minutes. The lens elongates, becomes surrounded by a clear zone, presumably a sol, formed from its own substance, is released from the pigment mass in which it is embedded and rounds up into a sphere which gradually wastes away as the zone of solution about it becomes indistinct. The brilliant red, central core flows out from the center of the melanosome (figs. TT, 4–7) and rounds up in several spherules. The melanosome also rounds up and the two colored masses very gradually waste away without imparting any recognizable tint to the surrounding water.

Occurrence.—Two specimens of this species were taken July 12, 1917, with a No. 25 net, in a haul 6 miles off La Jolla, California, in a haul from 80 meters to the surface and in a surface temperature of 20° C. The same day another individual was noted in a haul made on the previous day and kept in the laboratory over night. This was made at a distance of 4 miles off La Jolla, from 80 meters to the surface and in a surface temperature of 19°8 C.

Comparisons.—*E. extrudens* is the most highly specialized and widely divergent member of the subgenus *Erythropsis*, and is nearest of all its members to the subgenus *Polyopsidella*. The structural features indicating this are the detached pigment particles, the marked internal stratification of the lens suggesting a transition to or from the compound condition, the reduction in the size of the tentacular recess, and the oblique tentacle or prod. These features are not unlike the divided lens of *E. hispida*, the scattered pigment of *E. labrum*, and the reduced recess and oblique prod of *E. scarlatina*, all included in *Polyopsidella*. Since, however, its lens is not externally divided into separate lobes, *E. extrudens* is not placed in the subgenus with compound ocellus, but it is

evidently a transition form close to it. The ventral position of the prod is more marked than in any other species, and its differentiation into shaft, head, and stylet most complete, while the spiral tract on its surface was not detected in any other species.

## **Erythropsis hispida** sp. nov.

Plate 12, figure 127; text figure SS, 2

Diagnosis.—Medium sized species with ovoidal body, its length 1.46 transdiameter; girdle displaced 0.6 transdiameter; ocellus not protuberant, lens composed of a row of six spheroids at the left of the sulcus, pigment mass spheroidal, dark brown with brownish radiations; prod slender, not capitate, hispid, with short terminal stylet; peripheral vacuoles elongated, crowded, orange pink. Length, 89$\mu$. Pacific off La Jolla, California, August.

Description.—The body is ovoidal, its length 1.46 transdiameters, measured at the widest part, which is slightly above the equator. The dorsoventral diameter slightly exceeds the transverse. The epicone is much smaller than the hypocone and is shifted towards the right by the displacement of the girdle, which is about 0.6 transdiameter. The height of the epicone at the proximal end of the girdle is 0.12 of the total length of the body and 0.5 at its distal end. The apical region is highest at the left, slopes rapidly to the right and is less flattened than usual. No anterior horn was noted. The hypocone forms more than 0.75 of the body, is distended in an equatorial region on the sinistral face and is slightly flattened at the antapex, especially in lateral view.

The girdle forms a steep, descending left spiral, displaced distally 0.6 transdiameter. It is steepest in its distal region on the ventral face. Its two ends reach the median plane. The transverse furrow is very narrow, 0.04 transdiameter in width, and deeply impressed. The precingular groove runs subparallel to the girdle throughout its course, diverging anteriorly from it as it proceeds distally, from one width of the furrow at the proximal end to four widths at the distal end. The distal end of the groove turns abruptly anteriorly and appears to die out alongside the sulcus. The surface between this groove and the transverse furrow is broadly concave. No postcingular groove was noted. The sulcus begins at the summit of the epicone to the left of the main axis, curves to the right, joins the girdle, curves in a slight convexity to the right of the ocellus, joins the distal end of the girdle and merges in the deep, terminal, axial, tentacular recess. This cavity is 0.27 of the total length of the body in length and about 0.2 of the greatest diameter in width when it expands about the base of the tentacle. It contracts slightly midway of its length and flares distally into the posterior opening about 0.25 transdiameter across. The left flap of the sulcus folds slightly over the right, hiding the upper part of this tentacular recess.

The transverse flagellum does not completely encircle the body. No longitudinal flagellum was noted and an attachment area on the anterior lip of the distal end of the girdle was not detected.

The prod was not observed in full activity. As noted in the single individual of this species which we have seen it was a slender, almost cylindrical structure, located in the axis and directed posteriorly. Its total length, including the short stylet, was almost equal to the transdiameter and its diameter about 0.08 of the same. It has a globular enlargement at its base whose diameter is 1.5 that of the shaft. It enlarges slightly towards its distal end, but is only slightly capitate even when contracted. At the distal end it bears a short, acute stylet whose length does not exceed the diameter of the prod. Its axis contains a slender axial thread, the retractor

muscle, and the distribution of the fine points on its surface suggests the possession of circular contractile fibers, the protractor muscles. Its surface is everywhere covered, except at the tip, with minute pointed elevations, giving to it a characteristic hispid appearance, hence the specific name *hispida.* Upon the stimulus of contact the tentacle was contracted, growing stouter and more capitate as a result.

The ocellus is of the compound type, and is unique among the varied ocelli of this genus in that it consists of a row of lenses applied to one face of the pigmented sphere, with radial streamers. The lenses lie on the left side of the intercingular part of the sulcus immediately against its margin. Viewed from the left, as in our figure (pl. 12, fig. 127), they appear as flattened spheres whose diameter is slightly greater than that of the tentacle. When viewed more from the right it appears that their diameter in the transverse direction is nearly twice that in the vertical, that is, they are flattened ellipsoids. There are six of these lenses, subequal with the terminal ones, somewhat smaller, and all subject to irregularities in contour.

The pigment body is spheroidal, flattened on its right face where the lenses lie in contact with it. Its diameter is about 0.3 transdiameter of the body. At equidistant points on its circumference it sends off into the surrounding cytoplasm feathery tapering streamers of its substance, the longest of which are about equal to its radius in length. Its color is a brownish black with brownish core and streamers shading into brick red. It is noteworthy that the axis of the ocellus as a whole is here less definitely directed anteriorly than in the simple type of ocellus.

The periphery of the body after prolonged confinement under the cover glass presents a characteristically mottled appearance due to a reticulum of pale glaucous green cytoplasm containing in its meshes a salmon-pink fluid, tinged with aniline yellow, with a resulting pale cream tone to the body as a whole which has the usual glassy translucent texture prevalent in all the species of *Erythropsis.* A small pusule is connected with the tentacular recess with an accessory spheroidal one close at hand. Another similar sphere lies near the anterior flagellar pore, but no pusule connecting either with the pore or sphere was noted.

The nucleus is broadly ellipsoidal, with the major axis 1.25 the minor, and subparallel to the major axis of the body. It lies slightly anterior to the middle of the body. No moniliform chromatin threads were evident. No chromatophores or food balls were present.

DIMENSIONS.—Length of body, 89$\mu$; transdiameter, 61$\mu$; major axis of nucleus, 30$\mu$; length of tentacle, probably contracted, 55$\mu$; diameter of pigment body, 20$\mu$; of lenses, 6$\mu$ by 10$\mu$.

OCCURRENCE.—One individual taken in a haul of a No. 25 silk net 0.75 mile off La Jolla, California, August 13, 1917, from 83 meters to the surface in surface temperature of about 22° C. It occurred with *E. minor* and another undetermined species of *Erythropsis.*

COMPARISONS.—This species belongs to the subgenus *Polyopsidella* with compound lenses including *Erythropsis scarlatina, E. labrum,* and *E. richardi.* It is nearest in this particular to the first named, having six instead of five lenses in the row. It is unique in the radial processes from the pigment body and has the most asymmetrical epicone in the genus. The mottling of the surface is somewhat like that figured by Schütt (1895) for *Pouchetia* (= *Erythropsis*) *cochlea.* The tentacle is of the non-capitate form seen in *E. scarlatina, E. minor,* and *E. richardi,* but bears a terminal stylet as in *E. cornuta, E. minor,* and *E. extrudens,* and is posteriorly directed as in all species except *E. extrudens.* The species is unique in the genus in the pattern exhibited by the

peripheral vacuoles which are close set as in *E. cochlea* (Schütt), but throughout the surface the individual vacuoles exhibit an anteroposterior elongation wholly lacking in *E. cochlea*. The salmon-pink color is also unique.

### **Erythropsis labrum** sp. nov.

Plate 12, figure 132; text figure SS, 6

DIAGNOSIS.—Large sized species with ellipsoidal body, its length 1.33 transdiameters; girdle displaced 0.2 transdiameter; sulcus with overlapping, anteriorly directed flap on right side; ocellus deeply imbedded; lens composed of seven spheroids; pigment mass deeply and irregularly lobed, black, with yellow-ochre core and widely scattered granules; prod capitate, without stylet; peripheral vacuoles elongated longitudinally, scattered irregularly. Length, 111$\mu$. Pacific off La Jolla, California, August.

DESCRIPTION.—The body is broadly and not quite symmetrically ellipsoidal, its length 1.33 transdiameters measured at the widest part which is at the middle. The dorsoventral diameter is a trifle less than the transverse. The right side is evenly convex and the left and dorsal are somewhat flattened. The left side of the body extends somewhat farther posteriorly, as in the case of the left horn in *Ceratium*. The epicone is much flattened, forming a low cone whose base has a diameter of 0.7 transdiameter and an altitude at the proximal end of the girdle of 0.18 of the total length of the body and of 0.33 at the distal end on the right ventral side. Dorsally its lower margin scarcely lies below the summit so that its surface slopes mainly to the right and ventrally and constitutes as a whole less than 0.1 of the total surface. It has no distinct apical horn, although there is a slight hump at the right of the tip of the sulcus. The hypocone forms over 0.9 of the body, is slightly contracted posteriorly, and has a broadly rounded antapex, slightly cleft by a broad groove from the tentacular recess, with the lobe on the left about two widths of the furrow longer than that on the right.

The girdle ascends steeply from the anterior flagellar pore to almost the anterior margin along the dorsal side, then turns posteriorly with a reversed curve on the ventral face, so that the total intercingular displacement is about 0.22 transdiameter. It makes a complete turn around the body, but its junction with the sulcus is hidden by the anterior lobe of the flap of the right side of the sulcus. The furrow is rather deeply impressed and is about 0.03 transdiameter in width. It is paralleled by paracingular lines or precingular and postcingular grooves equidistant from the furrow, each about a width of the furrow removed from its margins.

The sulcus extends from apex to antapex, fading out anteriorly in a feebly marked loop at the left of an apical hummock, the homologue of the horn of *E. cornuta*. It makes a flat, reversed curve as it joins the girdle at the anterior flagellar pore, passes to the right of the lenses, joins the distal end of the girdle beneath the anterior flap, and then widens out into the deep, axially located, tentacular recess. This recess and the intercingular section of the sulcus are hidden beneath the widely overlapping right flap (hence the specific name *labrum*) which extends anteriorly as a free lobe from the distal end of the girdle, so far as to cover over the anterior flagellar pore. This flap is notched at the tip, which morphologically is near to the *posterior* border of the distal end of the girdle. The *anterior* border in this region in some species, as in *E. cornuta* (pl. 12, fig. 129), sometimes bears a notch which marks the attachment area where the anterior end, possibly the anterior horn, of the posterior schizont is attached to the body of its sister cell, the anterior schizont. It may well be that this notch in the posterior border is due to the same cause, the final attachment of the two parting schizonts (Kofoid and Swezy, 1917).

The tentacular recess is exceptionally deep in this species, reaching to the middle of the body, where it has a width of 0.16 transdiameter in the upper 0.4 of its length. Below this it flares in a campanulate outline beneath the left flap. The prod in the single individual seen was quiescent and apparently contracted. Its total length in this condition was 0.4 transdiameter. The smooth cylindrical shaft formed 0.5 its length and the ellipsoidal knob whose diameter was 1.5 times that of the shaft formed the other 0.5. There was no terminal stylet and no circular wrinkles were noted, but a sheath of longitudinal fibrillae lies near the periphery of the shaft.

The ocellus is of the compound type consisting of a group of about seven subspheroidal, transparent, hyaline lenses crowded in a loose mass opposite the intercingular region of the sulcus to the left of the flap. Their total volume is about the same as that of the single lens of such species as *E. richardi,* of approximately the same dimensions of body.

The pigment mass itself is black, irregularly lobed, and without fine processes. Twelve droplets of similar pigment are distributed in the peripheral plasma across the equatorial region of the ventral face. The core of the mass is an ellipsoidal (?) body, not fully exposed, extending beyond the anterior end of the pigment mass. It is of a dark yellow ochre color. As a result of the dispersal or absence of integration of lenses and pigment mass the ocellus extends for a distance of 0.5 transdiameter obliquely anteroposteriorly on the left ventral face of the body. The largest group of dispersed granules lies adjacent to the mass of lenses.

The nucleus is spherical, very hyaline, shows no trace of moniliform chromatin threads and is located in the left anterior region, extending far into the epicone. There are two pusules located respectively at the anterior flagellar pore and at the right of the tentacular recess. Both are linear and bifurcated and their distal ends almost coalesce. Several smaller detached vacuoles filled with a pinkish fluid similar to that in the pusules are present near the girdle on the ventral face.

The general color is a glaucous hyaline grey with a greenish tinge imparted by the peripheral vacuoles, which are rather large, ellipsoidal to linear in form, attaining a length of 0.2 transdiameter posterodorsally. More ellipsoidal or pyriform types appear on its ventral surface and a birfurcating, dendritic form was observed in the posterior part at the right of the sulcus. The periphery is thickly strewn with minute grey granules which have neither the color nor the consistency of the pigment grains.

DIMENSIONS.—Length, 111$\mu$; transdiameter, 88$\mu$; diameter of nucleus, 45$\mu$.

OCCURRENCE.—One individual was taken in a haul of a No. 25 silk net made August 10, 1917, one mile off La Jolla, California, from 50 meters to the surface and in a surface temperature of about 22° C. It occurred in the same catch with *E. hispida* and another undetermined species of *Erythropsis.*

COMPARISONS.—This species belongs to the subgenus *Polyopsidella,* but is unique in the subgenus in the degree of dispersal or lack of integration of the parts of the ocellus. The lens is not only organized in the largest number of parts but it is also most loosely assembled. The pigment mass is more deeply lobed and many more detached pigment granules are dispersed in the cytoplasm than in any other species in the genus. It is also unique in the presence of the anteriorly directed projection at the right of the sulcus over the intercingular gap.

The capitate form of prod links it with *E. pavillardi,* but it differs from this species in all other features. The divided lens is most like that of *E. hispida* or of *Pouchetia juno.* On the whole, next to *E. extrudens,* it is the most highly specialized species in the genus, though not the most aberrant one.

It might appear that this was a contracted individual of some other species with the ocellus in disintegration. However, the fact that in our experience this organ persists longer than any other structure after cytolysis, and the lack of any evidence that it disintegrates *in situ* prior to cytolysis, lead us to conclude that the lobed structure of the elements of the ocellus is not a mere artifact.

### **Erythropsis minor** sp. nov.

Plate 12, figure 131; text figure SS, 9

Diagnosis.—A small species with stout, pyriform, ventrally arched body; tapering hypocone; girdle displaced 0.45 transdiameter; ocellus 0.5 transdiameter in length with red core; lens and black melanosome each simple, hemisperical; prod short, tapering, with very short stylet. Length, 48µ. Pacific off La Jolla, California, July, August.

Description.—Body stout pyriform, asymmetrical, its length (excluding tentacle) 1.4 transdiameters at the widest part which is at the anterior end of the hypocone. Ventral surface concave, dorsal convex. Dorsoventral diameter 0.88 transdiameter. Epicone relatively large, its length, at right of sulcus, 0.5 transdiameter. There was no apical horn. Owing to the large size and protuberance of the ocellus the epicone on the left ventral region is scarcely exposed at all in ventral view and, as a whole, is pushed to the right and has little dorsal surface. The hypocone is widest a short distance below the girdle and contracts distally in an angle of about 30° to a rounded asymmetrical antapex. The right side is the longer, but the appearance of asymmetry is increased by the obliquity of the point of view in the drawing. It was less evident in other views and disappeared entirely as the animal rounded up prior to cytolysis.

The girdle is peculiar in not completely encircling the body and in having its proximal end almost at the anterior end at the left shoulder fully 0.25 transdiameter in the horizontal direction from its distal end. It descends rapidly in a left spiral so that the intercingular displacement is about 0.5 transdiameter in the vertical direction. The furrow has a fairly uniform width throughout of 0.09 transdiameter. Its lower margin extends considerably beyond the upper, and its trough is rather deeply indented. The transverse flagellum extends almost to the end of the girdle and arises from the anterior flagellum pore immediately in front of the lens. No paracingular grooves or bands were noted.

The sulcus begins near the center of the epicone, runs to the left to its junction with the girdle. It turns sharply to the right, following closely the contour of the ocellus, and joins the distal end of the girdle at the level of the lower edge of the melanosome, and extends directly posterior to the antapex. Its vertical displacement is 0.45 transdiameter, but the length of the oblique intercingular region is more than 0.5 transdiameter. It is a narrow channel throughout, but opens internally in the antapical region into the tentacular recess. This is very short, 0.27 transdiameter in length, and is broadly campanulate in form, its distal opening being 0.4 transdiameter across.

The prod is a slender regular conical structure of 10° with a rounded tip and minute terminal stylet asymmetrically located. It is not quite axial in position and inclines ventrally about 10° from the major axis. Its length when (fully?) extended was 0.75 and when contracted 0.4 transdiameter. No trace of longitudinal or circular fibers or of surface granulations was noted. A distinct longitudinal flagellum was found in this species. It persisted for some time, was noted in various positions of the body, and was active in propulsion of the body. It takes its origin from the posterior flagellar pore located on the dorsal wall on the right side of the tentacular recess behind and to the right of the prod a short distance within the recess. It was about twice as long as the prod.

The ocellus is relatively very large, its length is 0.55 transdiameter and its main axis inclines 45° to the right and ventrally from the major axis of the body. It protrudes considerably beyond the contour of the body, especially in ventral view, and crowds the intercingular sulcus anteriorly and the anterior flagellar pore almost to the anterior margin. The lens somewhat exceeds a hemisphere, its diameter is 0.35 transdiameter. It is composed of concentric laminae with a brilliant iridescence of spectral colors. The pigment mass is also regularly hemispherical without lobes or detached granules and receives the base of the lens in its flattened side. The black melanosome encloses a rather large coral-red core which shines through the thin layer of black pigment.

The nucleus is a very elongated ellipsoid placed transversely across the equatorial region. Its major and minor axes are 0.75 and 0.33 transdiameter respectively in length. It is possible that it is in transformation prior to mitosis. No chromatin net and perinuclear zone were noted. Pouch-shaped pusules with pinkish contents arise from the two flagellar pores. They are of equal size and 0.25 transdiameter in length. No food balls or vacuoles or chromatophores were found. Several greenish globules lie near the sulcus on the ventral face and a number of minute greenish vacuoles were scattered in the peripheral plasma. The general color was a pearl grey.

Dimensions.—Length, 48μ; transdiameter, 35μ; length of nucleus, 26μ; length of extended (?) tentacle, 26μ; length of ocellus, 19μ.

Occurrence.—Two individuals seen. These were taken with a No. 25 silk net in the Pacific Ocean off La Jolla on July 20 and August 13, 1917, respectively. The hauls were made from depths of 80 and 83 meters to the surface and in surface temperatures of 20°6 C and 21°7 C respectively.

Activities.—The individuals seen were not as active as those of *E. extrudens* or *E. pavillardi*, and the tentacle was subject to only feeble contractions as observed by us, although there was no evidence that this inactivity was due to the approach of cytolysis.

Comparisons.—This is the smallest species of the genus. It is possible that it is a juvenile stage of some other form, although the morphological evidence for structural transformations with growth as the individual grows older are slight among dinoflagellates. It is nearest to *E. cornuta* (Schütt) in structure, but is not only smaller, 48μ as compared to 104μ, but has a different type of prod, tentacular recess, shape of body and nucleus, and lacks the apical horn.

The position of the longitudinal flagellum at the right side of the tentacular recess and *behind* the prod is confirmed by the presence of the posterior pore and pusule. In Schütt's figure (1905, pl. 26, fig. 96) of *E. cornuta* the posterior flagellum is represented as arising at the base of and ventral to a spherical structure which we interpret as the capitate end of the prod. The flagellum figured by Schütt is remarkably stout and peculiarly wavy. It is possible that its origin is correctly figured; if so, the location of the posterior flagellar pore differs remarkably in different species of *Erythropsis*. It is also possible that its origin is dorsal to this tentacular knob, not ventral as figured. If so, this location is homologous to that in *E. minor*. It is possible that the extreme thickness of flagellum figured by Schütt is due to contraction and may not represent a frayed-out, axial tentacular fiber exposed by partial cytolysis, as its structure figured by Schütt might suggest. The undoubted presence of the

longitudinal flagellum in this species precludes all possibility that the tentacle represents in *Erythropsis* a modified form of the longitudinal flagellum of other Gymnodinioidae.

## **Erythropsis pavillardi** nom. sp. nov.

Plate 12, figure 133; text figures SS, 3, 5

*Erythropsis agilis,* Pavillard (1905), pp. 48–49, pl. 3, fig. 1.
*E. agilis,* Fauré-Fremiet (1914*c*), in part, pp. 27–47, pl. 1, text figs. 1, 3–12.

Diagnosis.—Small to medium sized species with ellipsoidal body, its length 1.3 transdiameters, curved apical horn; girdle displaced 0.8 transdiameter; protuberant ocellus, with hemispherical lens; flattened brownish-black pigment mass with red core; elongated, hispid, cylindrical tentacle attaining five times the length of body. Length, 55–82$\mu$. Mediterranean at Cette, October; Croisic, west coast of France, September; Pacific, off La Jolla, California, July.

Description.—The body is quite regularly ellipsoidal, its length 1.3 to 1.5 transdiameters; dorsoventral diameter slightly less than the transverse. The epicone is a low cone of about 120° with a height of about 0.5 transdiameter, except near the distal end of the girdle, where it slightly exceeds 0.75 transdiameter, or 0.5 the length. Its diameter at the base is about 0.8 transdiameter of the body. Its apex is rounded and bears a short, sinistrally directed, oblique apical horn standing at an angle of 30°–45° from the vertical. It has the appearance of protoplasmic undulations and has been figured by Pavillard (1905) and Fauré-Fremiet (1914) as carrying a median flagellum. This is either the displaced transverse flagellum, or is an appearance due to local protoplasmic undulations. Our observations are not conclusive on this point, but favor the latter view. The horn is retracted as cytolysis approaches. The hypocone forms about 0.75 of the total body, is somewhat more rotund on the right, and has the contour of a hemisphere in the antapical region.

The girdle forms a descending left spiral, descending steeply at its distal end to a total displacement in the intercingular region of 0.45 of the total length of the body or at least 0.66 transdiameter. In Pavillard's figure (text fig. SS, 5) there is a considerable displacement of the dorsal side. The girdle almost completely encircles the body. The furrow is broad and shallow, widening slightly beyond the anterior flagellar pore locatd above the ocellus. It is uniform in width thereafter, but constricts to a narrow slit as it enters the sulcus. No attachment area was noted at its distal end. The transverse flagellum extends at least half way around the body. No longitudinal flagellum was detected. An anterior paracingular line is clearly defined, with a flattened space equal to the furrow in width between it and the furrow. No posterior paracingular line was noted.

The sulcus is a narrow groove curved around the right side of the relatively large ocellus, extending as a narrow slit for a short distance below it and then widens out into the deep, axially located, campanulate, tentacular recess, which extends anteriorly for a distance of 0.35 of the total length of the body. The extension of the sulcus anteriorly upon the epicone is indicated by the location of what seems to be the transverse flagellum thrown forward to the apex from the anterior flagellar pore. Pavillard's (1905) figure suggests this also. There is, however, a possibility that the margins of the sulcus are here contractile. The tentacle is extraordinarily large in this species. When fully extended it is a fairly uniform cylinder attaining five times the length of the body. Pavillard (1905) figures it with a uniform diameter of 0.2 transdiameter when fully extended. We find it smaller (0.16–0.18 transdiameter) than this when contracted to one-fourth that length. When extended it is fairly uniform in caliber

throughout, but in contraction it swells out within the tenacular recess, and at the distal end to such a degree that the latter becomes somewhat capitate. There is no terminal stylet, the distal end being broadly rounded. There is a distinct axial, longitudinal strand, the retractor fiber and a series of equidistant circular fibers, the protractors. The prod was coarsely granular or hispid on its surface in Pavillard's specimen, but not in ours.

The ocellus lies to the left of the intercingular region of the sulcus, the anterior 0.8 of which it crowds to the right. Its total length is 0.55 transdiameter and the axis of the lens is about 45° from the major axis. The lens is hemispherical, as exposed, iridescent, and is buried rather deeply in the black-pigment mass. This is flattened, with its long axis passing obliquely postero-ventrally. It is somewhat more voluminous or swollen on the ventral and sinistral sides of the lens. No colored core was visible in our specimen, but Pavillard figures a yellowish-brown tint in its center. The ocellus as a whole is more than usually protuberant.

The nucleus is ellipsoidal (spherical in end view) and lodged far anterior in the epicone in the right dorsal region. Its major and minor axes are respectively 0.65 and 0.5 transdiameters in length. It is hyaline and does not exhibit the moniliform chromatin network usual in the dinoflagellates. The pusule arises from the anterior flagellar pore and extends posteriorly at the right of the ocellus toward the distal end of the girdle, with another branch running posteriorly from the pore along the dorsal side of the tentacular recess. In Pavillard's figure the two, posteriorly located, yellow bodies are probably food pellets. None occurred in our specimen. There were no peripheral vacuoles formed during our observations. The plasm was at all times a translucent, hyaline, dull opaline green, shading into variscite green. Fauré-Fremiet's (1914*c*) specimens had a faint pinkish tone.

DIMENSIONS.—Length of body, excluding prod, 82μ; including extended tentacle, 530μ; length of prod, extended, about 450μ; contracted, 90μ; transdiameter, 57μ; dorsoventral, 60μ; diameter of lens, 17μ. Pavillard's specimen was smaller, length, 55μ. Fauré-Fremiet gives a range of 50μ to 100μ in total length of body.

OCCURRENCE.—A single individual was taken off La Jolla, California, July 30, 1917, in a haul with a No. 25 net from a depth of 80 meters to the surface, made 2.5 miles offshore in a surface temperature of about 21° C. Pavillard (1905) observed a single individual taken in plankton from the Etang de Thau, a small bay from the Mediterranean at Cette, France, on October 19, 1904, in surface temperatures of 14°8 C. Fauré-Fremiet records (1914) a score of specimens from Croisic, on the west coast of France.

ACTIVITIES.—The individual observed by us was extraordinarily active. When first brought into view it was circling without noticeable rotation in anticlockwise spirals about six times its length in diameter. During this time and when at rest its prod underwent ceaseless rhythmical contractions, externally contracting to a length about equal to that of the body and extending as much as five times its length. The rapidity of contraction varied within short intervals. A number of records were made of the number of these contractions for given periods, as follows: 51 contractions in 30 seconds, or 1.7 per second; 27 in 10 seconds, or 2.7 per second; 35 in 20 seconds, or 1.7 per second; and 14 in 10 seconds, or 1.4 per second. These records were made at consecutive intervals during the course of a few minutes. They average 2.2 per second. The contractions slowed down and stopped some time before cytolysis occurred. It remained active for nearly six hours.

SYNONYMY.—Pavillard (1905) figures as *E. agilis* Hertwig a small species about half the size of Hertwig's, with more smoothly contoured body, more conical epicone, longer apical horn, more displaced girdle, and a black instead of a red pigment mass. In view of the degree of speciation detected by us in the genus and because of these differences above noted it seems probable that Pavillard had a different species from that found by Hertwig (1884) at Sorrento. It appears to be similar to one we have found at La Jolla. We take pleasure in naming it for Professor Pavillard, the investigator of the Dinoflagellata of the Mediterranean.

The *Erythropsis* which Fauré-Fremiet (1914*c*) discovered at Croisic, France, in 1913, and called *E. agilis* Hertwig, appears to be identical with that figured by Pavillard (1905) from Cette. We have elsewhere (1917) given the grounds upon which we reject Fauré-Fremiet's reversed orientation, origin and reversed direction of the transverse flagellum and the longitudinal flagellum emerging in the anterior loop of the sulcus from the apex. The red core or "Erythrosome" was more in evidence in his material than in ours, but in all other essential features except for those noted in our paper (1917) the similarity is sufficiently close to justify the inclusion of the *Erythropsis* from Cette, Croisic, and La Jolla in one species.

COMPARISONS.—Our specimen is not wholly in agreement in all details of structure with that found by Pavillard. Its girdle is apparently not so steep dorsally, its furrow is wider, its prod is not hispid and becomes capitate on contraction, and it is 82μ in length, while Pavillard's was only 55μ. However, the lens is the same, the pigment mass similar in form, though lacking the yellow to brown core as observed by us, and the tentacle and apical horn are alike in our two specimens in important respects. In view of the margin of difference to be allowed in accounts of organisms so difficult to observe accurately as this mobile genus, it seems best to accept these resemblances as indicative of specific identity and attribute our differences to divergences of observation and record, or to variation within the species.

*E. pavillardi* differs, in certain distinctive features, from *E. agilis* Hertwig, to which Pavillard (1905) referred his specimen, the third individual seen up to that time in the whole genus. The foremost of these is the red-pigment mass of *E. agilis* and the black one with yellowish-brown center of *E. pavillardi*. In addition Hertwig's species is about 100μ in length, while Pavillard's specimen was 55μ and ours 82μ. The antapex is truncate in *E. agilis* and rounded in *E. pavillardi*. In addition there are minor differences in shape of the epicone, course of the girdle, and exposure of the lens. As will be seen on comparison of the figures of all the species of the genus drawn to the same scale (text fig. SS), the distinctions between them are noticeable.

*E. pavillardi* belongs to the subgenus *Erythropsis* in restricted sense and is close to *E. minor*, but differs from it in longer prod without stylet and more rotund body of larger size. It is much smaller than *E. cochlea* and has a flattened instead of rotund pigment mass.

### **Erythropsis richardi** sp. nov.

Plate 12, figure 134; text figures SS, 10; VV

Diagnosis.—A large rotund species; body broadly ellipsoidal; its length 1.25 transdiameters; with low conical apical horn; girdle displaced 0.3 transdiameter: ocellus protuberant ventrally; lens compound; subhemispherical in two distinct sections; pigment mass slightly lobed with red core; prod (contracted) stout clavate with short asymmetrical stylet. Length, 106μ to 112μ. Pacific off La Jolla, California, August.

Description.—The body is very stout, rotund ellipsoidal, its length 1.18 to 1.25 transdiameters, according to the degree of contraction. Dorsoventral diameter equal to the transverse, left side more rotund and slightly longer. It is widest near the middle but in contracted condition it tends to bag out posteriorly and flatten anteriorly. Epicone low, flattened, its length middorsally, excluding horn, 0.1 transdiameter. Near the distal end of the girdle it extends posteriorly on the ventral side to nearly 0.5 the total length. The apex is almost squarely truncate with a small low conical apical horn whose height is about a girdle's width. The total volume of the epicone is less than 0.16 of that of the body. The hypocone is quite rotund, with rounded, indented, asymmetrical antapex with the left side the longer.

The girdle is almost flat for 0.75 of its course. It ascends slightly from the midventral flagellar pore to pass above the ocellus, then continues a horizontal course across the left and dorsal sides. At the right side it descends posteriorly at an angle of 45° across about 45° of the right ventral quadrant, then turns abruptly posteriorly for about 0.25 transdiameter, then turns again almost at a right angle and proceeds thence to its junction with the sulcus. No attachment area was noted at its distal end. The furrow is deeply incised and is bordered both anteriorly and posteriorly with a paracingular groove. The precingular groove originates about a furrow's width anterior to the proximal end of the girdle, increases its distance from the furrow to two furrows' widths in the dorsal region and to three or four at the distal end of the girdle. The postcingular groove is quite uniformly separated by a furrow's width from the girdle and has a ragged appearance. The paracingular bands or strips between grooves and the girdle are clear and free from surface markings and vacuoles and their surfaces are flattened or even slightly concave. They are clearly defined in this species.

The sulcus is little disturbed by the crowding of the ocellus upon it, and is thrown into only a slight sigmoid curve by its presence. It appears to extend upon the epicone to the base of the apical horn and probably to the left of it, is closely appressed in the intercingular region, and is without lateral overlap, being in fact open by a rather wide gap into the tentacular recess. This cavity extends into the axis of the body for 0.45 of its length and flares widely to 0.5 transdiameter at the antapical region (text fig. SS, 10).

The prod or tentacle is a stout clavate structure, withdrawn within the recess in the resting, contracted condition in which its greatest diameter, located near its middle, is 0.17 transdiameter. It is axially located, posteriorly directed, and tapers distally to a blunt point which bears a minute, asymmetrically placed, terminal stylet. When feebly extended it takes the form of a slender asymmetrical rod continued posteriorly from a swollen base and when completely retracted rounds up into a capitate knob (text figs. SS, 10) with or without a tip. There is a faint axial retractor fiber. No circular fibers are evident and the external surface is without granulations.

The ocellus is of the compound type, though less evidently so than any of the species of the subgenus *Polyopsidella*. It is displaced well to the left, about 0.17 transdiameter to the left of the sulcus with its main axis parallel to that of the body. It protrudes strongly on the ventral

surface. The lens is composed of two flattened superposed iridescent hemispheres, the front one 0.3 and the rear one 0.25 transdiameter in diameter, but not deeply imbedded in the pigment mass. This mass is broadly ellipsoidal, 0.35 transdiameter in length and slightly lobed. Its core is of a bright coral-red color which shines through the enveloping black pigment.

After cytolysis the ocellus (text fig. VV, 2) persists for a time. The melanosome contracts and exposes a third disklike segment of the lens of the same hyaline nature as the second segment. It is immediately against this that the coral-red core lies. The elements of the ocellus slowly waste away by peripheral solution and fragmentation, the pigment of the melanosome and the red globules of the core persisting longest.

The large spheroidal nucleus lies in the left anterior part of the body dorsal to the ocellus. It showed no beaded chromatin thread and was very hyaline, but after cytolysis it was seen to have an exceedingly fine beaded chromatin network and a distinct outer perinuclear membrane and inner hyaline zone. No pusule or food balls were noted. The peripheral plasma was filled shortly before cytolysis with a layer of small, uniform, rather closely packed, greenish vacuoles, present everywhere except in the paracingular bands. The general color was a pale glaucous green. There were no chromatophores.

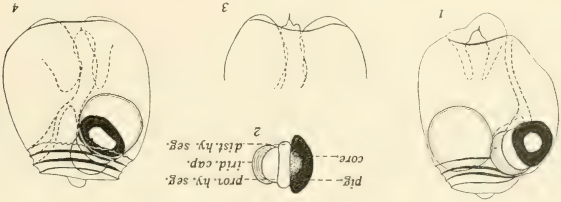


Fig. VV. Details of ocellus and tentacle of *Erythropsis richardi*. 1. Ocellus as revealed by cytolysis. Abbreviations: *irid. cap.*, iridescent stratified cap; *dist. hy. segt.*, distal hyaline segment exposed when in place in the body; *prox. hy. segt.*, proximal hyaline segment, imbedded in the pigment mass in the body but exposed by contraction or solution of the pigment at cytolysis; *core.*, coral-red core within the pigment; *pig.*, black pigment mass or melanosome. 2. Dorsal view of body showing retracted tentacle in capitate form. 3. Postero-sinistral view exposing opening of tentacular recess and contracting tentacle. 4. Contracted tentacle in lobed state seen from the dorsal side. × 500.

Dimensions.—Length, 106–112$\mu$; transdiameter, 85$\mu$; diameter of nucleus, 40$\mu$; of lens, 27$\mu$; of pigment body, 30$\mu$.

Occurrence.—Two individuals seen, taken in the plankton 3 and 4 miles off La Jolla, July 26 and 27, 1917, in hauls of a No. 25 silk net from a depth of 80 meters to the surface in surface temperatures of 21°4 C and 21°7 C.

Named for Professor Richard Hertwig of the University of Münich, the discoverer of *Erythropsis*. The preoccupation of the specific name *hertwigi* by a slip of the pen on the part of Jollos (1910, p. 203) precludes the use of the patronymic name of this eminent protozoologist as a specific name by us in *Erythropsis*.

Activities.—One individual was kept under observation from 11 a.m. till 2 p.m., when it underwent cytolysis. During this time it was feebly active, moving in irregular anticlockwise spirals in an intermittent fashion. The tentacle was not at any time in intense activity such as that shown by *E. pavillardi*.

A few feeble strokes with an extension of the tip only a little beyond the body were repeated from time to time. There was other evidence of a moribund condition. These observations suggest that the tentacle is small and less active in this species than in many others of the genus.

Comparisons.—This species belongs to the subgenus *Polyopsidella* because of its compound ocellus, but is most like the subgenus *Erythropsis* in that its compounding is least marked, being shown by three subdivisions of the lens and slight lobing of this pigment mass.

It is the only species with compound ocellus and also an apical horn. Its paracingular grooves and beads are more marked than usual in the genus. Its small, uniform, crowded peripheral vacuoles resemble those of *E. cochlea*, but are not appressed into polygonal fields as in that species. Its tentacle when extended resembles that of *E. cornuta* (Schütt), but its proportions, ocellus, girdle, and apical horn are quite different from those of that species.

## **Erythropsis scarlatina** sp. nov.

Plate 12, figure 128; text figures RR, 2; SS, 4

Diagnosis.—Large species; body elongated subcylindrical; its length 1.7 transdiameters; epicone reduced; its diameter 0.5 transdiameter; no apical horn; sides furrowed; girdle displaced distally beyond the middle; tentacular recess oblique; prod sinuous tapering; directed obliquely ventrally; no stylet; ocellus compound; lens of five segments in a row; black-pigment mass lobed; body extensively streaked and mottled with scarlet. Length, 104$\mu$. Pacific off La Jolla, California, August.

Description.—This species is unique in form, structure, and color. The body is elongate subcylindrical, somewhat truncate at both ends. Its length is 1.7 transdiameters and its dorsoventral diameter is slightly greater than the transdiameter. The epicone is reduced to an apical button whose diameter is only 0.5 transdiameter and altitude only 0.07, except in the distal quadrant in which it forms a long triangular process extending posteriorly along the right side of the sulcus for a full transdiameter from the apex. The center of the epicone is filled with a lone, rounded terminal knob which probably represents the apical horn. The hypocone forms over 0.9 of the body, its length at the anterior flagellar pore being 0.9 of the total length. Anteriorly its shoulders are rounded in abruptly to the girdle, about twice as far on the right as on its left side. The left margin is quite regularly convex while the right and dorsal are straight or even somewhat concave. The antapex is truncate, its outline being somewhat sinuous as a result of the posterior terminations of the lateral furrows. The sides of the hypocone are deeply scored by parallel grooves which run from the anterior shoulders to the postmargins. There are five of these on either side of hypocone. They are about equidistant and are deepest near the middle of the body.

The girdle forms a flat spiral around the button-like epicone with little deflection in its proximal 0.75. At the beginning of the distal quadrant it turns posteriorly at an angle of 45°, and steepens to 15° from the vertical near its distal end which is in consequence carried posteriorly to the middle of the body with a total displacement of 0.7 transdiameter. The furrow is very narrow, only about 0.05 transdiameter wide, and lies in the hollow of a deep depression.

The anterior flagellar pore lies in its proximal end a short distance in front of the lens and the transverse flagellum runs less than 0.75 of the length of the girdle. No paracingular grooves or bands were noted, and no attachment area detected.

The sulcus begins on the epicone above the girdle where it partially encircles the terminal knob, and after its junction with the girdle it passes in almost a straight line posteriorly. It is not displaced to the right by the deeply buried ocellus which somewhat underlies its intercingular region. It is a narrow slit closed by the overlapping right flap which forms a sharp salient angle at the upper end opposite the proximal end of the girdle. Posteriorly it opens out into the large posteroventral tentacular recess. This cavity has an extreme length at the ventral surface of 0.3 total length of the body and about half this on its dorsal side. From the middle of its sloping anterior surface springs the prod.

The prod, owing to the fact that the tentacular recess is not axially located but lies in the ventral half of the body and has a sloping anterior wall, projects ventroposteriorly at an angle of about 15° from the axis. It has a total length of about 0.75 transdiameter and projects for about half its length beyond the margin of the recess. Within this cavity it has a thickened shaft about 0.15 transdiameter in thickness, a constricted base, a somewhat sinuous course, and is reduced to about one-third of this diameter in its extruded part which likewise has a sinuous course. Its tip is blunt, without stylet and no circular or axial fibers were noted. No longitudinal flagellum was observed.

The ocellus is of the compound type. It consists of a segmented lens and lobed pigment mass. Its total length is 0.65 transdiameter, and its major axis is somewhat oblique to that of the body. The lens consists of five rounded disks, appressed in a linear series decreasing a trifle in size posteriorly, set slightly oblique to the main axis and parallel to and beneath the sulcus. Their color is a clear glaucous blue with a tinge of yellow. Their diameter is 0.15 to 0.18 transdiameter and their thickness one-third to one-half their diameter. They rest lightly along a part of the flattened face of the irregularly hemispherical pigment mass, and not in continuation of its axis as is usually the case in the relation of lens and pigment. The pigment mass is bluntly lobed in several regions and a small detached mass lies anterior to the line of lenses. The pigment mass proper consists of an outer melanosome of black pigment and an inner core of reddish-brown substance almost entirely concealed by the darker material.

Pigment is found elsewhere in the body of this remarkable animal distributed in a very characteristic and peculiar fashion. The periphery of the epicone and shoulders of the hypocone are covered with a mantle of brilliant Brazil-red pigment distributed in the peripheral plasma as a mottled reticulum formed of finely divided granules. These red reticulations extend posteriorly down the ventral face on either side of the sulcus and become continuous with a radial network of similar pigment spreading in all directions from a denser center near the base of the tentacle. Several droplets of dark clear rose-red pigment lie on the left side of the sulcus posterior to the ocellus, and a single large droplet of the same sort is found near the proximal end of the girdle. Several linear masses of reddish-black pigment lie in the axis of the distal part of the tentacle. This pigment appears, in the main, to be distributed in regions of presumably greatest tension and most active oxidative processes, namely, the base of the prod, and along the girdle and sulcus. There is no indication that this pigment is derived from the food of the organism.

The ellipsoidal nucleus has major and minor axes with lengths of 0.55 and 0.35 transdiameter respectively and lies with the major axis at an angle of 45° to that of the body, far anterior. No chromatin net was detected in its hyaline interior. There were no chromatophores or food balls, rhabdosomes or peripheral vacuoles. No pusules were noted. The cytoplasm was highly translucent of a clear pearl-grey color, shading into a glaucous blue in the margins and along the lateral grooves.

Dimensions.—Length, 104$\mu$; transdiameter, 59$\mu$; length of tentacle, 48$\mu$; of ocellus, 36$\mu$.

Occurrence.—A single individual was taken in a haul of a No. 25 silk net 5 miles off La Jolla, California, on August 21, 1917, from a depth of 83 meters, in surface temperature of about 22° C.

Activities.—The animal was not motile during the period of observation. There was no indication that the lateral grooves were due to collapse, or abnormal, or moribund condition.

Comparison.—This is the most unique species of the genus in form, color, and structure, being most divergent in all structural features, such as ocellus, tentacle, and pigmentation. The lateral grooves recall those of *Amphidinium cucurbita* and *Gymnodinium puniceum* in location, form, and number. No other species of *Erythropsis* has any suggestion of such grooves, although indications of longitudinal lines of stress are hinted at in the tendency for peripheral vacuoles to take on longitudinally elongated forms. No other species of *Erythropsis* has any finely distributed pigment outside of the pigment mass and none has the divided lenses in a linear series, except *E. richardi*, in which there are only two segments to the lens. Owing to these structural features, *E. scarlatina* stands apart from all other species as the most specialized representative in the subgenus *Polyopsidella*, of which it is the type species.

## SUMMARY

1. This monograph includes all known unarmored and free-living Dinoflagellata. It is based on a study of the marine forms of the San Diego region made at the Marine Biological Station of the Scripps Institution for Biological Research. It includes 223 species belonging to 16 genera.

2. The following genera are new: *Protodinifer, Gyrodinium, Torodinium, Pavillardia, Protopsis, Nematodinium,* and *Proterythopsis.*

3. One hundred and seventeen species are new, distributed as follows in the genera: *Protodinifer,* 1; *Amphidinium,* 12; *Gymnodinium,* 36; *Gyrodinium,* 23; *Cochlodinium,* 21; *Torodinium,* 1; *Pavillardia,* 1; *Protopsis,* 1; *Nematodinium,* 2; *Pouchetia,* 12; *Proterythropsis,* 1; *Erythropsis,* 6; a total of 117 new species.

4. The Dinoflagellata have evolved from a primitive, biflagellated flagellate, by differentiation of the two primitive, similar, anterior flagella. One becomes ribbon-like, with short undulations, and is the transverse flagellum of the Diniferidia. The other flagellum becomes the longitudinal trailing flagellum by the posterior migration of the flagellar pore to the midventral region. In the Adiniferidea the flagella are differentiated but the pore has not migrated posteriorly.

5. The unarmored forms are more primitive than the armored ones, the Athecatoidae than the Thecatoidae in the Adiniferidea, the Gymnodinioidae than the Peridinioidae in the Diniferidea.

6. The new genus *Protodinifer* is a primitive form with anterior, differentiated flagella, and partial girdle feebly developed. It shows affinities to the Adiniferidea and suggests the origin of both Adiniferidea and Diniferidea from unarmored, ancestral forms allied to it.

7. The two flagella, transverse and longitudinal, with the two channels in the surface of the body in which they lie, the girdle and sulcus, are superficial organs in active contact with the environment, and are extensively modified in an orthogenetic manner in the evolution of the genera, and in speciation within the genera.

8. The modifications consist of a progressive elongation of the girdle, with accompanying torsion of the body in a left spiral up to four turns. There is also a progressive torsion of the sulcus and its prolongation to the apex and antapex, culminating in the genus *Cochlodinium.*

9. Structural differentiations of the areas bordering the girdle and sulcus, with or without torsion, appear in the pseudopodia of *Gymnodinium zachariasi*, the ephemeral (?) tentacle of *G. pseudonoctiluca*, the tentacle of *Noctiluca*, the incipient prod of *Proterythropsis*, and the highly developed prod and its enclosing chamber in *Erythropsis*. There is also a tendency for pigment to aggregate in the margins of the girdle, for the stigma to appear in the sulcus, and for the ocellus to lie adjacent to the girdle.

10. There is an orthogenetic evolution of the ocellus in the genera *Protopsis*, *Pouchetia*, *Proterythropsis*, and *Erythropsis*, by the integration of scattered pigment granules and loosely aggregated lens bodies into a compact melanosome enclosing a red sensory core at the base of concentrically laminated, spherical lens.

11. Nematocysts are formed in *Polykrikos* and *Nematodinium*. They are derivatives of the centrosome or cell center.

12. There is an extraordinary range in color of the Gymnodinioidae. The simpler forms are green, yellow, or brown, while the colors of many of the more complex ones are near the red end of the spectrum.

13. Holozoic nutrition occurs in most of the genera and is almost exclusively prevalent in those of a higher type. The sulcus is the cytosome.

14. *Noctiluca* belongs in the Gymnodinioidae. It has a sulcus, the so-called atrium and rod organ, a rudimentary girdle, heretofore undetected, and the transverse flagellum is present in a rudimentary condition in the so-called tooth.

15. The Cystoflagellata, as defined by Haeckel, should be reduced to contain only *Leptodiscus* and *Craspedotella*, pending the analysis of their affinities when their life history shall be discovered.

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# INDEX

PLATE 1

## EXPLANATION OF PLATES

All figures are made with the aid of a camera lucida from living material by the authors and colored by Miss Anna Hamilton, unless otherwise stated.

### PLATE 1

Fig. 1. *Amphidinium asymmetricum* sp. nov. Camera drawing by Miss Inez Smith. Ventral view. Note the single large, ramifying chromatophore obscuring the centrally located nucleus. × 1323.

Fig. 2. *Gymnodinium lineatum* sp. nov. Ventral view. The surface striae show the unusual obliquity characteristic of the species. Note the branching pusule and the aggregated pigment at the antapex. × 626.

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Fig. 4. *Amphidinium galbanum* sp. nov. Ventral view. The surface is lightly furrowed and immediately beneath it are the green, leaflike chromatophores. The nucleus is posteriorly located. × 1102.

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Fig. 6. *Amphidinium cucurbitella* sp. nov. Dextroventral view. Surface deeply furrowed. Two large food masses present, one recently ingested, surrounded by a water vacuole which has disappeared in the second food body. × 626.

Fig. 7. *Gymnodinium scopulosum* sp. nov. Sinistroventral view. An encysted individual with cytoplasm unusually free from the products of metabolism. The size of the cyst indicates an advanced stage of encystment. × 1102.

Fig. 8. *Cochlodinium schuetti* sp. nov. Sinistroventral view. Note the single large food body, the minute oil droplets in periphery, and the two pusules merged into one. × 1102.

Fig. 9. *Amphidinium cucurbita* sp. nov. Ventral view. Compare the complex cytoplasmic structure with the simpler condition in *Amphidinium galbanum* (fig. 4). The nucleus is the reniform body dorsad to the posterior pusule. Surface deeply striate. × 626.

Fig. 10. *Gymnodinium ravenescens* sp. nov. Ventral view. Two food bodies present with chromatophores. Note the similarity of chromatophores with those of *Amphidinium corpulentum* (fig. 11). × 1102.

Fig. 11. *Amphidinium corpulentum* sp. nov. Ventral view. Note the presence here also of food bodies or the products of metabolism and chromatophores, indicating both holozoic and holophytic nutrition. The nucleus is the long, ellipsoidal body on the right side. × 1323.

Fig. 12. *Gymnodinium situla* sp. nov. Ventral view. Note the colored food bodies, vacuoles and spherules, products of metabolism. Nucleus is posteriorly located. × 1102.


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PLATE 2

PLATE 2

Fig. 13. *Amphidinium pacificum* sp. nov. Colored by O. Swezy. Ventral view. Note the refractive granules, probably the products of metabolism, and chromatophores in the body. × 626.

Fig. 14. *Gymnodinium bicorne* sp. nov. Camera drawing by Miss Ruth Merrill. Lateral view. × 1102.

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Fig. 25. *Cochlodinium faurei* sp. nov. Dextroventral view. Note abundance of food bodies and oil droplets in cytoplasm, products of metabolism. × 1102.


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PLATE 3

## PLATE 3

Fig. 26. *Gymnodinium amphora* sp. nov. Ventral view. The peripheral layer of color is shown only at the margins. Note the fatty, refractive bodies, rodlets, etc., with brownish food mass near the center. × 626.

Fig. 27. *Gymnodinium incisum* sp. nov. Colored by O. Swezy. Ventral view. Note the partly digested *Pouchetia* with ocellus nearly intact. × 1102.

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PLATE 4

## PLATE 4

Fig. 35. *Gymnodinium dissimile* sp. nov. Colored by O. Swezy. Ventral view. × 1102.

Fig. 36. *Amphidinium vasculum* sp. nov. Colored by O. Swezy. Ventral view. Note the differentiated ectoplasm, food bodies and radial rodlets. Nucleus is spheroidal body in posterior part. Compare with *Gymnodinium dogieli* (pl. 3, fig. 34). × 626.

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Fig. 40. *Gymnodinium lunula* Schütt. Encysted stage prior to formation of zooids. × 1102.

Fig. 41. *Gymnodinium canus* sp. nov. Ventral view. Nucleus lies between girdle and posterior flagellar pore. Fatty globules and other products of metabolism present. × 626.

Fig. 42. *Gymnodinium sphaericum* sp. nov. Ventral view. Body somewhat distorted. Predivision stage of nucleus. Cytoplasm filled with rodlets and other products of metabolism. × 1102.

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Fig. 44. *Gymnodinium herbaceum* Kofoid. Original drawing by C. A. Kofoid; colored by O. Swezy. Note food vacuoles filling the cytoplasm with chromatophores also present. × 881.

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Fig. 49. *Torodinium robustum* sp. nov. Colored by O. Swezy. Viewed from left side. Elongate pusule. × 1102.


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PLATE 5

## PLATE 5

Fig. 50. *Gyrodinium melo* sp. nov. Ventral view. Note the presence of both food bodies and green chromatophores. Girdle is verging towards the *Cochlodinium* type. × 1102.

Fig. 51. *Gymnodinium puniceum* sp. nov. Ventral view. Cytoplasm is filled with food bodies. Nucleus lies on the left side of the body, posterior to the girdle. × 1102.

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Fig. 53. *Cochlodinium augustum* sp. nov. Ventral view. Food body present. Nucleus is ellipsoid near center of body. This species represents the maximum of torsion of the body in the group. × 1102.

Fig. 54. *Gyrodinium capsulatum* sp. nov. Ventral view. Note the double cyst enclosing the body. Surface color shown only at the margins. This approaches the *Gymnodinium* type of girdle. × 1102.

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Fig. 57. *Gymnodinium doma* sp. nov. Ventral view. Food body present. Note the unusual size of the pusule. Peripheral color shown only at margins. × 626.

Fig. 58. *Gymnodinium ovulum* sp. nov. Ventral view. Large food mass nearly fills body. × 1102.

Fig. 59. *Gymnodinium multiliniatum* sp. nov. Ventral view. Note peripheral zone of rodlets. × 626.

Fig. 60. *Cochlodinium clarissimum* sp. nov. Ventral view. Note the peripheral zone of pink vacuoles. The body at the left is the nucleus. Long ellipsoidal food body near it. × 1102.


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PLATE 6

## PLATE 6

Fig. 61. *Pouchetia maxima* sp. nov. Viewed from right side. Food bodies present. Note the posterior vent through which a food mass has been ejected. This cytoplasmic skirt is soon withdrawn. × 626.

Fig. 62. *Gyrodinium maculatum* sp. nov. Dextroventral view. Large food body present. Violet-colored pigment abundant. × 1102.

Fig. 63. *Gymnodinium abbreviatum* sp. nov. Ventral view. Food bodies present. Note irregularities in the surface due to the superficial alveolar layer. × 1102.

Fig. 64. *Gyrodinium postmaculatum* sp. nov. Ventral view. Antapical agglomeration of pigment. × 722.

Fig. 65. *Gymnodinium lineopunicum* sp. nov. Viewed from right side. Epicone occupied by an ingested *Pouchetia*. Pomegranate-purple pigment abundant. × 722.

Fig. 66. *Pouchetia subnigra* sp. nov. Viewed from right side. Note strands of melanin granules. Nucleus greatly elongated. × 603.

Fig. 67. *Cochlodinium radiatum* sp. nov. Ventral view. Food body present. Note the pusular canal connecting both pores, peripheral splashes of aster-purple pigment abundant. × 1102.

Fig. 68. *Nematodinium partitum* sp. nov. Viewed from the right side. Note the ingested *Gymnodinium*. Nematocysts present. Diffuse type of ocellus. × 837.

Fig. 69. *Gymnodinium violescens* sp. nov. Ventral view. Food bodies present. Nucleus is ellipsoidal body in the center. Violet pigment abundant. × 1102.


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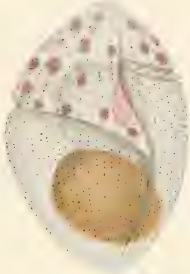
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PLATE 7

## PLATE 7

Fig. 70. *Gyrodinium fulvum* sp. nov. Sinistroventral view. Surface is heterostriate. Note unusual development of anterior pusule. The longitudinal flagellum was attached at its tip to small particle and vibrated in a cone, following the direction of the arrow. $\times$ 1102.

Fig. 71. *Cochlodinium atromaculatum* sp. nov. Ventral view. Melanin granules present along girdle. Nucleus is long ellipsoidal body centrally located, cytoplasm filled with colorless vacuoles. $\times$ 626.

Fig. 72. *Gyrodinium spumantia* sp. nov. Ventral view. Cytoplasm foamlike, completely filled with vacuoles, nucleus spheroidal near the center. $\times$ 626.

Fig. 73. *Gyrodinium flavidum* sp. nov. Ventral view. Cytoplasm filled wtih vacuoles of varying sizes. $\times$ 626.

Fig. 74. *Protodinifer tentaculatum* sp. nov. Viewed from left side. Note stout, posterior prod, large food body and other products of metabolism. Girdle is short, fading dorsally. $\times$ 1102.

Fig. 75. *Gymnodinium cinctum* sp. nov. Colored by O. Swezy. Ventral view. Cyst closely investing body. Note unusual shape of pusule and peripheral chromatophores. $\times$ 1102.

Fig. 76. *Gyrodinium ochraceum* sp. nov. Ventral view. Surface striate, nucleus centro-anterior, pusules connected by slender canal. Pigment in granules scattered through peripheral zone. $\times$ 626.

Fig. 77. *Gyrodinium culeus* sp. nov. Ventral view. Cytoplasm foamlike, nucleus dorsad of anterior flagellar pore. Note rose-red pigment granules. $\times$ 1102.

Fig. 78. *Cochlodinium distortum* sp. nov. Colored by O. Swezy. Viewed from right side. Nucleus anterior, pigment granules strung on surface striae. Probably a somewhat distorted specimen. $\times$ 626.

Fig. 79. *Cochlodinium citron* sp. nov. Viewed from left side. Nucleus anterior. Note numerous oil droplets, rodlets, and other products of metabolism in cytoplasm. $\times$ 1102.

Fig. 80. *Cochlodinium pulchellum* Lebour. Colored by O. Swezy. Dextrodorsal view. Note unusual length of girdle and amount of torsion of body. Nucleus posterocentral. $\times$ 1102.

Fig. 81. *Gyrodinium dorsum* sp. nov. Ventral view. Nucleus in posterior half of body, food body in anterior part. $\times$ 1102.

Fig. 82. *Gyrodinium ochraceum* sp. nov. Dextroventral view. Individual after the pigment granules (fig. 76) had collected into band along the girdle. This later pinched off small granules until it presented the same appearance as in figure 76. $\times$ 626.


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PLATE 8

## PLATE 8

Fig. 83. *Gymnodinium sulcatum* sp. nov. Colored by O. Swezy. Ventral view. Food body present. Hypocone marked by yellowish ridges. Rose-red coloring collected into granules at apices. × 1102.

Fig. 84. *Pouchetia purpurescens* sp. nov. Viewed from right side. Camera drawing by Miss Pirie Davidson; colored by O. Swezy. Yellow-ochre food body. Note unusual position of ocellus at right of sulcus. × 1102.

Fig. 85. *Cochlodinium rosaceum* sp. nov. Viewed from left side. Individual with ingested *Pouchetia* which is enclosed in food vacuole. Body is somewhat distorted. × 1102.

Fig. 86. *Gymnodinium rubrum* sp. nov. Ventral view. Perinuclear zone present. Rose-red pigment abundant. Girdle verging towards the *Gyrodinium* type. × 626.

Fig. 87. *Pouchetia purpurata* sp. nov. Viewed from left side. Food body present. Note strings of melanin granules. × 1102.

Fig. 88. *Gymnodinium rubricauda* sp. nov. Ventral view. Food bodies present. Colored pigment aggregated into granules. × 1102.

Fig. 89. *Pouchetia voracis* sp. nov. Sinistroventral view. Note the double cyst enclosing this individual. Food bodies present near ocellus. Superficial layer of rose red shown only at margins. × 1102.

Fig. 90. *Pouchetia rubescens* sp. nov. Dextrodorsal view. Food bodies present. × 583.

Fig. 91. *Gyrodinium postmaculatum* sp. nov. Ventral view. Food bodies present. Superficial layer of color not fully shown except at margins. × 1102.


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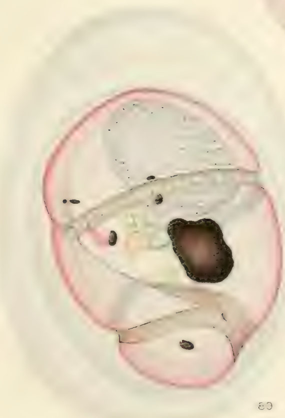
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PLATE 9

## PLATE 9

Fig. 92. *Cochlodinium helix* (Pouchet) Lemm. Viewed from right side. Large food body present. Pusules connected by canal. × 1102.

Fig. 93. *Cochlodinium cavatum* sp. nov. Viewed from left side. Organism enclosed in double cyst. Note ventral excavation of body. × 1102.

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Fig. 97. *Gymnodinium hamulus* sp. nov. Camera drawing by Miss Inez Smith. Ventral view. Nucleus is spheroidal body near anterior flagellar pore. × 1102.

Fig. 98. *Amphidinium turbo* sp. nov. Colored by O. Swezy. Ventral view. × 1102.

Fig. 99. *Cochlodinium turbineum* sp. nov. Viewed from right side. Remains of yellow-ochre food body in cytoplasm. × 1102.

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Fig. 101. *Cochlodinium pirum* (Schütt) Lemm. Unusual size of nucleus may be preparatory to division. × 1102.

Fig. 102. *Gyrodinium caudatum* sp. nov. Ventral view. Note the unusual type of cyst. Food bodies present. × 1102.

Fig. 103. *Gyrodinium obtusum* nom. sp. nov. Colored by O. Swezy. Ventral view. Pusules connected by slender canal. × 1102.

Fig. 104. *Cochlodinium virescens* sp. nov. Ventral view. Food bodies present. Pusules connected by canal. × 1102.

Fig. 105. *Cochlodinium catenatum* Okamura. Colored by O. Swezy. Chain of four zooids. × 626.

Fig. 106. *Gyrodinium ovoideum* sp. nov. Colored by O. Swezy. Ventral view. Food body present. × 626.


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PLATE 10

## PLATE 10

Fig. 107. *Cochlodinium miniatum* sp. nov. Camera drawing by Mrs. J. R. Michener. Viewed from lateral side. Food bodies present. Nucleus is large body centroposterior, adjacent to brownish food mass. Coral-red pigment. × 626.

Fig. 108. *Cochlodinium volutum* sp. nov. Note unusual branching of anterior pusule. Nucleus is anterior. × 1102.

Fig. 109. *Gyrodinium herbaceum* sp. nov. Camera drawing by Miss Pirie Davidson. Dextroventral view. Nucleus anterior, food body posterior. × 1102.

Fig. 110. *Gymnodinium submarinum* sp. nov. Ventral view. Nucleus elongate near center of body. Food body present. × 1102.

Fig. 111. *Amphidinium dentatum* sp. nov. Ventral view. Note enlarged, connected pusules. Nucleus sinistrocentral. Peripheral green chromatophores. × 1102.

Fig. 112. *Gyrodinium virgatum* sp. nov. Ventral view. Note the asymmetrical posterior end. Nucleus surrounded by perinuclear, vacuolate zone. Coral-red pigment. × 1102.

Fig. 113. *Cochlodinium scintillans* sp. nov. Viewed from right side. Food bodies present. × 1102.

Fig. 114. *Pavillardia tentaculifera* sp. nov. Viewed from right side. Peripheral color shown only at margins. Note peculiar type of nucleus. × 1102.

Fig. 115. *Cochlodinium convolutum* sp. nov. Dextroventral view. Predivision stage of nucleus. Note elongated cyst. × 1102.

Fig. 116. *Gyrodinium rubricaudatum* sp. nov. Ventral view. Note antapical agglomerated pigment. × 672.

Fig. 117. *Gyrodinium corallinum* sp. nov. Ventral view. Note peripheral, vacuolate zone of nucleus. Coral-red pigment abundant. × 626.

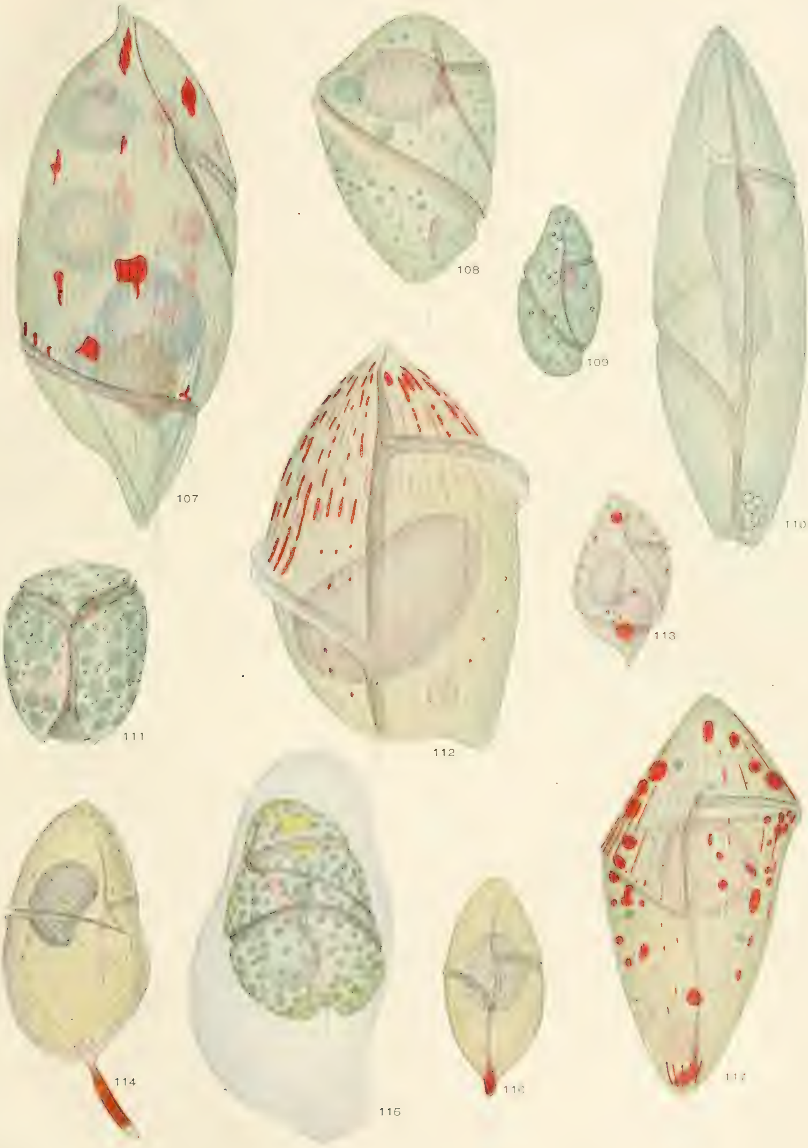
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PLATE 11

## PLATE 11

Fig. 118. *Pouchetia violescens* sp. nov. By an oversight the complete outline of the lens was omitted. Viewed from right side. Food body present. Transverse flagellum thrown forward into sulcus. Pigment diffuse. × 626.

Fig. 119. *Pouchetia maculata* sp. nov. Viewed from right side. Food body present. Black pigment abundant. × 1102.

Fig. 120. *Pouchetia violescens* sp. nov. Viewed from left side. Pigment was diffuse, as in figure 118, when first noted, but it soon began to collect into masses and strands, leaving the cytoplasm colorless. Black is omitted from melanosome in the figure. × 626.

Fig. 121. *Pouchetia alba* sp. nov. Dextrodorsal view. Nucleus anterior. Food bodies present. Note diffuse type of melanosome. × 626.

Fig. 122. *Nematodinium armatum* (Dogiel). Viewed from right side. Nucleus anterior. Nematocysts conspicuous. × 626.

Fig. 123. *Proterythropsis crassicaudata* sp. nov. Viewed from right side. Food body present. × 1102.

Fig. 124. *Nematodinium torpedo* sp. nov. Dorsal view. Food bodies present. Nematocysts anterior. × 1102.

Fig. 125. *Pouchetia poucheti* sp. nov. Dextroventral view. Nucleus is ellipsoidal body near center. Food bodies present. Note diffuse type of ocellus. × 1102.

Fig. 126. *Pouchetia atra* sp. nov. Dorsal view. Predivision stage of nucleus. Food body present. Note presence of granules thrown out of the body but still retained in the cyst. × 1102.

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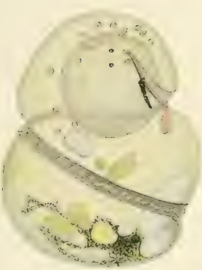

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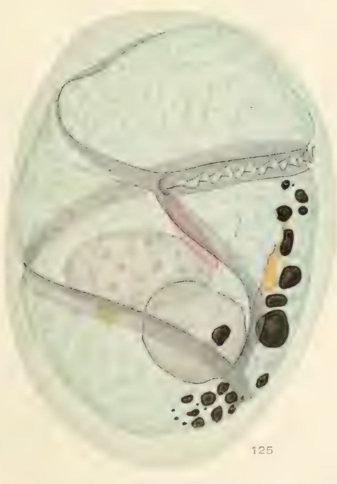

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PLATE 12

## PLATE 12

Fig. 127. *Erythropsis hispida* sp. nov. Ventral view. Note peripheral reticular layer. Nucleus dorsad to ocellus. × 626.

Fig. 128. *Erythropsis scarlatina* sp. nov. Dextroventral view. Pigment in prod. Nucleus anterior. Profuse scarlet pigment peripheral anteriorly, in center of cytoplasm posteriorly. × 626.

Fig. 129. *Erythropsis cornuta* (Schütt). Dextroventral view. Pusules connected by slender canal. Transverse flagellum thrown forward out of girdle. Retractor fibrillae extend forward from prod. × 626.

Fig. 130. *Erythropsis extrudens* sp. nov. Viewed from right side. Transverse flagellum thrown forward out of girdle. Pusules branched. × 626.

Fig. 131. *Erythropsis minor* sp. nov. Ventral view. Transverse flagellum thrown forward out of girdle. Posterior flagellum present. × 1102.

Fig. 132. *Erythropsis labrum* sp. nov. Ventral view. Prod strongly retracted, showing fibrillae. Diffuse type of ocellus. Branched pusules. Cuticular markings of pale green. × 626.

Fig. 133. *Erythropsis pavillardi* nom. sp. nov. Viewed from right side. Prod extended, showing fibrillae. Transverse flagellum thrown out of girdle. Ocellus integrated, conspicuous. × 626.

Fig. 134. *Erythropsis richardi* sp. nov. Ventral view. Prod retracted. Nucleus dorsad to ocellus. Cuticular layer of pale, blue-green bodies. × 626.

127 128 129 130 131 132 133 [illegible]